

THE BIOSYSTEMATICS OF *CALYLOPHUS* (ONAGRACEAE)¹

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ABSTRACT

The genus *Calylophus* (Onagraceae), a segregate of *Oenothera*, was studied in reference to systematic relationships, breeding systems, pollination, and cytology. Six species are recognized, four in sect. *Salpingia*: *C. tubicula*, *C. hartwegii*, *C. toumeyii* and *C. lavandulifolius*, and two in sect. *Calylophus*: *C. berlandieri* (formerly *C. drummondianus*) and *C. serrulatus*. Several changes in nomenclature and rank are made. Crosses performed among species demonstrated strong barriers to hybridization between the two sections of the genus and slight to moderate barriers among species within sections.

Populations of *Calylophus* are distributed through the Great Plains, the southwestern United States, and northern Mexico. The various taxa occupy distinct habitats which range from xeric sites in the Chihuahuan Desert to relatively mesic pine and pine-oak forests. In most forms of the genus, the plants are suffrutescent perennials and occupy calcareous soils. One form is restricted primarily to gypsum soils.

Cytological investigations showed a remarkable degree of translocation heterozygosity in natural populations of *Calylophus*. Translocations were observed in all taxa, with 75% of 183 plants (excluding *C. serrulatus*) exhibiting heterozygosity for at least one translocation. Numerous plants were heterozygous for more than one translocation, and the mean number per plant was 1.3. *Calylophus serrulatus* is a complex structural heterozygote and all individuals observed were heterozygous for at least five or six translocations. Hybridization experiments with *C. berlandieri* suggested that *C. serrulatus* maintains structural hybridity with gametophytic lethals in pollen and embryo sacs.

The basic chromosome number of the genus is $x = 7$. Tetraploidy was observed in individuals from 5 of 62 populations of *C. hartwegii* that were examined. A few plants of several taxa possessed diminutive chromosomes ranging from 1 to 11 in number. The most frequent observation was of a single dark-staining pair in addition to the normal complement.

Chromosome observations of hybrids showed profound intersectional differences in structure, primarily from translocations. Translocation differences are also marked among populations in sect. *Calylophus*, but are slight among the taxa of sect. *Salpingia*.

The breeding systems of *Calylophus* are varied, with *C. serrulatus* self-compatible and highly autogamous and the other species self-sterile. *Calylophus berlandieri* and *C. tubicula* have short floral tubes, strong ultraviolet contrast patterns, matinal anthesis, and are visited by a variety of diurnal insects. Anthesis of the remaining members of sect. *Salpingia* occurs in the afternoon or evening. These plants possess long floral tubes, variable ultraviolet contrast patterns, and are visited by sphingid moths and crepuscular bees in numbers that vary from locality to locality.

Biosystematic studies of the genus *Calylophus* were begun in 1967, shortly after it had become apparent that this genus constituted a natural group no less distinct from *Oenothera* than from other genera of the tribe Onagreae (Raven, 1964). This paper is based on those studies and on an examination of extensive

¹ This study was initiated as a doctoral dissertation at Stanford University (Towner, 1970b), and subsequently amplified. I would like to express great appreciation to Peter H. Raven, at whose suggestion this research was begun. His advice and generous assistance have been invaluable throughout the course of the study. He, D. E. Breedlove, and D. P. Gregory provided both material of *Calylophus* and unpublished information on pollination. Sharon Stewart gave me indispensable assistance in the field, laboratory, and greenhouse. Dan Holmes and Judith Lynch assisted me in the field. Steven and Ann Seavey were most helpful in the maintenance of cultivated plants and the handling of herbarium material. John H. Thomas directed the processing of herbarium loans. The illustrations of flowers were drawn by Julie Spranza.

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herbarium material. A preliminary publication stemming from this research (Towner & Raven, 1970) was based on a less complete study of herbarium material and some of the taxonomic decisions made then are changed in the present paper.

The genus *Calylophus* is distinguished from the other genera of the Onagreae by the following suite of characteristics: a peltate stigma which may be discoid or nearly square in shape, sometimes with 4 shallow, broad lobes; microsporogenous tissue divided into packets in the locules of the anthers; yellow flowers; and a many-seeded capsule. In the opinion of Raven (1964), *Calylophus* is most closely related to those genera of the Onagreae which share the feature of divided microsporogenous tissue: i.e., *Gaura*, *Clarkia*, *Heterogaura*, and perhaps *Hauya*. The genus occurs over much of the Great Plains, extending into the mountains of the Great Basin region and other parts of the Southwest, and also reaching southward to the Mexican Plateau. The area of greatest diversity for the genus includes West Texas, southern New Mexico, and north-central Mexico. Populations are usually colonial and widely scattered, often occurring in disturbed areas. Habitats occupied by the species of *Calylophus* are typically somewhat xeric plains or hills with soil that is often calcareous. Plant associations in which the various forms occur range from creosote bush scrub in the Chihuahuan Desert to pine forests of several types.

The history of the genus *Calylophus* has involved several transfers at the generic level as various authors have seen fit to separate the group from *Oenothera* or to unite the two genera. Traditional treatments of the species here considered have placed them in *Oenothera* subgenera *Salpingia* and *Calylophus* or in the respective genera *Galpinsia* and *Meriolix*. Rafinesque (1819) was the first to distinguish a species of what is now *Calylophus* from *Oenothera*, although his publication, lacking a description of the genus, was invalid. The name *Meriolix* was validated only later, by Endlicher, in 1840. *Calylophus*, the first generic name of legitimate publication, was presented by Spach (1835a) and emended by him to "*Calylophis*" without justification in the same year (Spach, 1835b). It thus has priority over *Meriolix*, *Galpinsia*, and *Salpingia* at the generic level. Most of the nineteenth century treatments of the species of *Calylophus* retained them in *Oenothera*. In the late nineteenth century and until quite recently, the generic names *Meriolix* and *Galpinsia* were frequently used for the various species of *Calylophus* in treatments such as those of Heller, Small, and Rydberg.

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During the nineteenth century the explorations and collecting of Nuttall, Wright, Lindheimer, Berlandier, Hartweg, Fendler, James, Cockerell, and Toumey provided type material for most of the presently known taxa in the genus. All taxa now considered valid, except *Calylophus hartwegii* subsp. *macartii* and *C. tubicula* subsp. *strigulosus*, were described and published between 1817 and 1898. Over this period and during the early twentieth century a number of names were proposed for minor variants, especially by L veill , Small, and Nelson. These contributed additional confusion to the taxonomy of the genus, which in any circumstance would have been difficult to interpret. The situation was greatly improved with the publication of Munz's (1929) revision of these species, a treatment which brought together the information available at that time and gave relative order to the taxonomy of the group. Many superfluous names were reduced to synonymy and for the first time decisions were based on adequate herbarium material. Some of the species boundaries remained unclear even then because of the complexity of variation in sect. *Salpingia*, an erroneous appraisal of the type of *C. hartwegii*, and the absence of information on breeding systems in the *C. serrulatus* group.

Raven's (1964) paper, which brought this group of species together as the genus *Calylophus*, was closely followed by the publication of Shinnery (1964). Shinnery presented a taxonomy similar to that used here, except that the facts concerning breeding systems in *C. serrulatus* were not yet known, and that some differences in the ranking of taxa exist between our treatments. Other differences include my recognition of *C. hartwegii* subsp. *fendleri* and a revised interpretation of *C. hartwegii* subsp. *hartwegii* and *filifolius*. In 1965 Munz published a monograph of the North American Onagraceae (Munz, 1965) in which the species of *Calylophus* were referred back to *Oenothera* and in which specific status was granted without justification to several of the entities presented by Munz as subspecies in 1929. Otherwise the taxonomy remained the same as in the earlier publication.

A brief taxonomic treatment of this group by Towner & Raven (1970), the basis of my account for the *Manual of the Vascular Plants of Texas* (Towner, 1970a), considered the species as belonging to *Calylophus*. The present work generally retains the same boundaries between taxa used in that paper. Exceptions include two changes in rank, the recognition of *C. tubicula* subsp. *strigulosus*, the reduction of *C. australis* to synonymy with *C. serrulatus*, and the changes in the names for the outcrossing members of sect. *Calylophus*. All of the foregoing changes were found necessary after a more thorough study of herbarium material was completed. *Calylophus lavandulifolius* and *C. toumeyii* were determined to be well differentiated from *C. hartwegii* and thus deserving of specific rank. *Calylophus serrulatus* is here judged to be possibly of multiple origins, and the series of populations once referred to as *C. australis* is now thought to be distinguished from other such series only by its geographical separation from the range of the rest of the species. Lastly, *C. berlandieri* was found to be the appropriate name for the entity treated by Towner and Raven as *C. drummondianus*. Type material of Drummond's was determined by an examination of pollen fertility to belong with the complex structural heterozygote *C. serrulatus*.

CYTOLOGY

Meiotic chromosome configurations were determined to establish the frequencies of structural and numerical changes in natural populations of *Calylophus*. Further, the cytology of experimental hybrids was observed in order to describe chromosomal differentiation among taxa in the genus. Previous reports of cytology in *Calylophus* (as species of *Oenothera*) include those of Hagen (1950), Lewis et al. (1958), Gregory & Klein (1960), and Kurabayashi et al. (1962). These authors reported translocation heterozygosity, tetraploidy, and extra chromosomes. P. H. Raven (personal communication) later established the presence of complex structural heterozygosity in the genus. Those phenomena were confirmed and their taxonomic distribution described in the present study. Inversion differences among populations were also found. Table 1 and the systematic accounts of the various taxa combine my findings and the results of earlier investigations.

Translocation heterozygosity is extremely common in the genus and was found in all taxa. *Calylophus serrulatus*, with its system of complex structural heterozygosity, consistently forms rings of 12 or 14 chromosomes at meiotic metaphase I. All other species form multivalent associations regularly. Excepting tetraploids and *C. serrulatus*, 130 of 183 plants (71%) had visible translocations, and in this sample the mean number per plant was 1.3. The most frequent number of translocations per plant was 1, but individuals with 2 or 3 were common. In one observation from *C. hartwegii* subsp. *filifolius* and two from *C. berlandieri* subsp. *berlandieri*, plants were heterozygous for 5 translocations. Directed alternate disjunction seems to prevail since translocation heterozygosity does not appreciably lower pollen fertility in natural populations. Heterozygosity may well be maintained in populations by the action of heterosis, deleterious recessive genes, or even balanced lethals, especially in taxa such as *C. berlandieri* where translocation heterozygotes comprised 85% of all plants examined. In its high frequency of naturally-occurring translocations, *Calylophus* resembles some species of *Gaura* (Raven & Gregory, 1972b), *Clarkia amoena* (Lehm.) Nels. & Macbr. subsp. *amoena* (Håkansson, 1942), and some populations of *Clarkia unguiculata* Lindl. (Lewis, 1953) among the Onagraceae.

Tetraploidy was observed sporadically in some subspecies of *Calylophus hartwegii*, but nowhere else in the genus. Seven populations of *C. hartwegii* subsp. *hartwegii*, *pubescens*, *maccartii* and intermediates among them were tetraploid ($n = 14$). These plants all showed a combination of bivalents and multivalents in meiosis. No taxon was found to be wholly tetraploid, and any evolutionary significance is probably minor. Tetraploid individuals appear to arise within populations from time to time.

Extra, diminutive chromosomes were found in several taxa from both sections of *Calylophus*, and could well occur in all of the taxa. They are small dark-staining bodies that often appear to be heteropycnotic and tend to proceed through first meiotic prophase and metaphase more rapidly than the normal chromosomes. Pairing between diminutives was common, and possible associations with the larger chromosomes were seen occasionally. The most frequent observation consisted of a single diminutive pair in addition to the normal comple-

TABLE 1. Cytology of natural populations of *Calylophus*^a

Locality	Collection	Observations
<i>C. berlandieri</i> subsp. <i>berlandieri</i> (22 populations)		
New Mexico De Baca Co. Eddy Co.	130 <i>Munz & Gregory</i> 23359 21	7 ₁₁ (2 plants); 4 ₁₁ + 1 ring of 6; 2 ₁₁ + 1 ring of 4 + 1 ring of 6 3 ₁₁ + 1 ring of 8 (G) 7 ₁₁ ; 5 ₁₁ + 1 ring of 4; 2 ₁₁ + 1 ring of 4 + 1 ring of 6 + 2 dimins.
Oklahoma Harmon Co. Jackson Co. Tillman Co.	87 138 140	4 ₁₁ + 1 ring of 6 $n = 7$ (5 ₁₁ + ?) 4 ₁₁ + 2 rings of 4; 1 ₁₁ + 1 ring of 4 + 1 ring of 8 + 1 to 2 supernumeraries
Texas Brooks Co. Calhoun Co.	60 61 177 179	probable 7 ₁₁ 4 ₁₁ + 1 chain of 6 + 2 dimins. 3 ₁₁ + 2 rings of 4 + 2 dimins.; 2 rings of 4 + 1 ring of 6 5 ₁₁ + 1 ring of 4; 2 ₁₁ + 1 ring of 4 + 1 ring of 6 4 ₁₁ + 2 ₁ + 1 ring of 4
Garza Co. Hartley Co. Hemphill Co. Kenedy Co.	<i>Raven & Gregory</i> 19304 <i>Roberts</i> 35 <i>Delso</i> 122 186 192	1 ₁₁ + 1 ? ring of 4 + 1 ? ring of 8 2 ₁₁ + 1 ring of 4 + 1 ring of 6 3 ₁₁ + 2 rings of 4 7 ₁₁ + 1 dimin.; 5 ₁₁ + 1 ring of 4 + 1 dimin.
Lipscomb Co. Ochiltree Co. Potter Co. Victoria Co.	<i>Rowell</i> 10414 158 91 <i>Bohart & Thorp</i> 650928-1	7 ₁₁ ; 5 ₁₁ + 1 ring of 4 (3 plants) 3 ₁₁ + 2 rings of 4; 1 ₁₁ + 1 ? ring of 12 5 ₁₁ + 1 ring of 4; 3 ₁₁ + 2 rings of 4 5 ₁₁ + 1 ring of 4; 1 ₁₁ + 1 ring of 4 + 1 ring of 8; 1 ₁₁ + 2 rings of 6 + 2 dimins.
Willacy Co. Wilson Co.	190 191 <i>Munz & Gregory</i> 23443	4 ₁₁ + 1 ring of 6 1 ₁₁ + 1 ? ring of 12 5 ₁₁ + 1 ring of 4 (G); 2 _n = 14 + 2 extra (K); 2 _n = 14 + 4 extra (K)
<i>C. berlandieri</i> subsp. <i>pinifolius</i> (23 populations)		
Oklahoma Custer Co. Lincoln Co.	154 149	3 ₁₁ + 2 rings of 4; 4 ₁₁ + 1 ring of 6 1 ₁₁ + ? ring of 12

TABLE 1. (continued)

Locality	Collection	Observations
Logan Co.	Raven & Gregory 19462 151 152	5 ₁₁ + ? ring of 4 5 ₁₁ + ? ring of 4; 3 ₁₁ + 2 rings of 4 3 ₁₁ + 2 rings of 4
Texas		
no locality	M. V. Brown	7 ₁₁ (L & B)
Bastrop Co.	H. & M. Lewis 1636	4 ₁₁ + 1 ring of 6 (L)
Baxar Co.	Klein 1671	7 ₁₁ (R)
	Klein 1672	5 ₁₁ + 1 ring of 4 (R)
	Klein 1674	3 ₁₁ + 2 rings of 4 (R)
	66	1 ₁₁ + 3 rings of 4
Blanco Co.	67	5 ₁₁ + 1 ring of 4
Brown Co.	72	3 ₁₁ + 2 rings of 4
Erath Co.	T. & L. Mosquin 5490	5 ₁₁ + 1 ring of 4 (R)
Gillespie Co.	Klein 1667	5 ₁₁ + 1 ring of 4 (R)
Hays Co.	Emory, no number (greenhouse voucher 67181)	3 ₁₁ + 1 ? ring of 8
	Raven & Gregory 19368	
	Gregory 419	4 ₁₁ + 1 ring of 6; 3 ₁₁ + 1 ring of 8
	Klein 1668	5 ₁₁ + 1 ₁ + 1 ring of 3 (or 4 ₁₁ + 1 ₁ + 1 ring of 5)
Kendall Co.		7 ₁₁ (R)
McCulloch Co.	Munz & Gregory 23431	2 ₁₁ + 1 ring of 4 + 1 ring of 6 (G)
Menard Co.	Raven & Gregory 19273	7 ₁₁ ; 5 ₁₁ + 1 ring of 4 (3 plants); 5 ₁₁ + 1 ring of 4 + 1 to 2 dimins.
Mills Co.	71	4 ₁₁ + 1 ring of 6
Wilbarger Co.	77	4 ₁₁ + 1 ? ₁₁ + 1 ? ring of 4
	C. hartwegii subsp. fendleri (15 populations)	
Arizona		
Apache Co.	112	5 ₁₁ + 1 ring of 4 + 2 to 4 dimins.; 3 ₁₁ + 1 ring of 4 + 1 chain of 4
New Mexico		
Chaves Co.	Munz & Gregory 23346 ^b	5 ₁₁ + 1 ring of 4 (G)
Grant Co.	244	3 ₁₁ + 2 rings of 4
Otero Co.	253	5 ₁₁ + 1 ring of 4; 3 ₁₁ + 2 rings of 4
Sorocco Co.	119	5 ₁₁ + 1 ring of 4
Torrance Co.	121	5 ₁₁ + 1 ring of 4

TABLE I. (continued)

Locality	Collection	Observations
Oklahoma Greer Co.	123	5 _{II} + 1 ring of 4; 3 _{II} + 2 rings of 4
	79	4 _{II} + 1 ring of 6; 5 _{II} + ?
	81	7 _{II}
	85	5 _{II} + 1 ring of 4 + 4 dimins.
	86	7 _{II} ; 5 _{II} + 1 ring of 4
Texas Presidio Co.	Parnell 68-T-30	7 _{II}
	R. C. Jackson in 1964	7 _{II} ; 5 _{II} + 1 ring of 4
	26	5 _{II} + 1 ring of 4; 5 _{II} + 1 ring of 4 + 4 to 5 dimins.
	27	7 _{II} (3 plants)
		<i>C. hartwegii</i> subsp. <i>filifolius</i> (8 populations)
New Mexico Chaves Co. Eddy Co.	128	$n = 7$
	Munz & Gregory 23357	2 _{II} + 1 ring of 4 + 1 ring of 6 (G)
	19	3 _{II} + 2 rings of 4
	22	5 _{II} + 1 ring of 4
Otero Co.	Munz & Gregory 23335	3 _{II} + 2 rings of 4 (G); 7 _{II}
	194	5 _{II} + 1 ring of 4
Texas Ward Co. Winkler Co.	Raven & Gregory 19159	3 _{II} + 2 rings of 4
	Irving 69	7 _{II} + 1 to 2 dimins.; 1 _{II} + 1 ring of 12 + 1 dimin.; 5 _{II} + 1 ring of 4 + 9 dimins.; 3 _{II} + 2 rings of 4 + 7 to 11 dimins.
		<i>C. hartwegii</i> subsp. <i>hartwegii</i> (11 populations)
Mexico Aguascalientes Chihuahua	McVaugh 16680	$n = 14$, e.g., 4 _{II} + 2 _{IV} + 2 _{VI}
	Breedlove 14305	7 _{II}
	249	7 _{II} + 2 dimins.; 5 _{II} + 1 ring of 4
	250	7 _{II}
	252	7 _{II} + 4 dimins.; 5 _{II} + 1 ring of 4
	Breedlove 5947	7 _{II} ; 5 _{II} + 1 ring of 4
Durango	Breedlove 14305A	7 _{II} (3 plants); 5 _{II} + 1 ring of 4 + 1 dimin.; 5 _{II} + 1 ring of 4 + 2 dimins.

TABLE 1. (continued)

Locality	Collection	Observations
Zacatecas	<i>Wiens</i> 3464 <i>Breedlove</i> 14338 <i>Breedlove</i> 14344 <i>Breedlove</i> 15485	7 _{II} (R) $n = 14$ 7 _{II} ; 5 _{II} + 1 ring of 4 5 _{II} + 1 ring of 4
Mexico	<i>C. hartwegii</i> subsp. <i>maccartii</i> (10 populations)	
Coahuila	53	7 _{II} ; 7 _{II} + 1 dimin.; 5 _{II} + 1 ring of 4 (2 plants)
Nuevo León	<i>Waterfall</i> 13215	$n = 14$, e.g., 5 _{II} + 3 _{IV} + 1 _{VI}
Tamaulipas	36, 38	7 _{II} ; 5 _{II} + 1 ring of 4
Texas	35	7 _{II}
Kinney Co.	<i>Strother</i> 299	7 _{II} ; 7 _{II} + 1 dimin.; 5 _{II} + 1 ring of 4 (2 plants)
Maverick Co.	34	5 _{II} + 1 ring of 4
San Patricio Co.	<i>Raven & Gregory</i> 19386	3 _{II} + 2 rings of 4 (2 plants)
Val Verde Co.	32	7 _{II}
	33	7 _{II}
Zapata Co.	<i>Perez</i> 42	$n = 14$, e.g., 10 _{II} + 2 _{IV}
	<i>C. hartwegii</i> subsp. <i>pubescens</i> (18 populations)	
Arizona		
Cochise Co.	5, 7	$n = 7$; 3 _{II} + 2 rings of 4
	161	5 _{II} + 1 ring of 4
Santa Cruz Co.	105	3 _{II} + 2 rings of 4
New Mexico		
Chaves Co.	12	7 _{II}
	13	7 _{II}
	94	7 _{II}
Quay Co.		
Oklahoma		
Custer Co.	<i>Munz & Gregory</i> 23508	$n = 7$ (K)
Greer Co.	82	5 _{II} + ? ring of 4; 2 _{II} + 1 ring of 4 + 1 ring of 6
Texas		
Brewster Co.	<i>Munz & Gregory</i> 23395	2 _{II} + 1 ring of 4 + 1 ring of 6 (G)
Coleman Co.	75	$n = 7$
Concho Co.	<i>Munz & Gregory</i> 23425	5 _{II} + 1 ring of 4 (G)

TABLE 1. (continued)

Locality	Collection	Observations
Culberson Co.	Munz & Gregory 23364	4 ₁₁ + 1 chain of 6 (G)
Irion Co.	Raven & Gregory 19211	5 ₁₁ + 1 ring of 4; 3 ₁₁ + 2 rings of 4
Pecos Co.	Munz & Gregory 23405	n = 14, e.g., 3 ₁₁ + 2 _{IV} + 1 _{VI} + 1 _{VIII}
Potter Co.	92	5 ₁₁ + 1 ring of 4
Terrell Co.	T. & L. Mosquin 5638	7 ₁₁ (R)
	Gregory 275	7 ₁₁ ; 5 ₁₁ + 1 ring of 4; 3 ₁₁ + 1 ring of 8
Wheeler Co.	88	5 ₁₁ + 1 ring of 4
	Miscellaneous <i>C. hartwegii</i> (6 populations)	
Arizona		
Pinal Co.	Lewis 1079	n = 7 (L)
	(betw. <i>hart.</i> and <i>pub.</i>)	
	3	5 ₁₁ + 1 ring of 4; 2n = 19 to 22
	(betw. <i>hart.</i> and <i>pub.</i>)	
New Mexico		
Guadalupe Co.	Munz & Gregory 23516	5 ₁₁ + 1 ring of 4 (G)
	(betw. <i>pubesc.</i> & <i>filif.</i>)	
Mexico		
Coahuila	39	n = 14, e.g., 10 ₁₁ + 1 ? _{VIII}
	(betw. <i>macc.</i> & <i>filif.</i>)	
Texas		
Brewster Co.	Munz & Gregory 23401	n = 14 (K)
	(betw. <i>hart.</i> and <i>pub.</i>)	
	Munz, no number	7 ₁₁ (H)
	(no voucher seen)	
Uvalde Co.		
	<i>C. lavandulifolius</i> (7 populations)	
Arizona		
Coconino Co.	114	n = 7
Navajo Co.	115	7 ₁₁ + 2 dimins.
Colorado		
Dolores Co.	Anderson 3138	5 ₁₁ + 1 ring of 4
Texas		
Brewster Co.	29	7 ₁₁ ; 5 ₁₁ + 1 ring of 4 (2 plants)

TABLE 1. (continued)

Locality	Collection	Observations
Nevada Clark Co.	101 104	7 ₁₁ ; 2 ₁₁ + 1 ring of 4 + 1 ring of 6 5 ₁₁ + 1 ring of 4 + 4 dimins.
White Pine Co.	Anderson 2897	3 ₁₁ + 2 ? rings of 4; 2 ₁₁ + 1 ring of 4 + ? ring of 6 + 2 dimins.
No locality Canada	<i>C. serrulatus</i> (30 populations)	
Manitoba	<i>Bandar</i>	ring of 14 (R)
	<i>Marshall 65-1</i> <i>Marshall 65-3</i>	probable ring of 14 probable ring of 14
Kansas Ford Co. Riley Co.	159 <i>Raven & Gregory 19483</i> <i>Anderson 2416</i>	probable ring of 14 probable ring of 14 probable ring of 14 probable ring of 14 (2 plants)
Scott Co. New Mexico	160	
Chaves Co. De Baca Co. Roosevelt Co.	134 131 132 133	ring of 14 (2 plants) 1 ₁₁ + probable chain of 12 ring of 14 (2 plants) ring of 14
Oklahoma Blaine Co. Greer Co.	153 80 83	ring of 14 probable ring of 14 probable ring of 14
Lincoln Co.	147 148	probable ring of 14 probable ring of 14
Logan Co. Murray Co.	150 145 146 155	probable ring of 14; 1 ₁₁ + probable ring of 12 probable ring of 14 ring of 14 probable ring of 14
Roger Mills Co. South Dakota	<i>Mosquin & Mulligan 5160</i>	ring of 14 (R)
Lawrence Co. Texas	<i>Raven & Gregory 19393</i> 182	chain of 14; probable ring of 14 probable ring of 14; 1 ₁₁ + probable ring of 12
Aransas Co.		

TABLE 1. (continued)

Locality	Collection	Observations
Cameron Co.	187	ring of 14
	188	probable ring of 14; 1 ₁₁ + probable ring of 12
Cochran Co.	136	probable ring of 14
Jackson Co.	175	1 ₁₁ + ring of 12 + 2 dimins.
Matagorda Co.	174	possible ring of 14
San Patricio Co.	184	ring of 14 (2 plants); chain of 14
Wyoming		
Niobrara Co.	Mosquin & Mulligan 5142	ring of 14 (R)
		<i>C. toumeyi</i> (2 populations)
Arizona		
Cochise Co.	106	3 ₁₁ + 2 rings of 4
	107	3 ₁₁ + 2 rings of 4; 4 ₁₁ + 1 ring of 6
		<i>C. tubicula</i> subsp. <i>strigulosus</i> (1 population)
Mexico		
Nuevo León	<i>U. of Kansas Exped. 119</i>	3 ₁₁ + 2 rings of 4 (2 plants)
		<i>C. tubicula</i> subsp. <i>tubicula</i> (9 populations)
New Mexico		
Eddy Co.	Munz & Gregory 23350, 23353	5 ₁₁ + 1 ring of 4 (2 plants; G)
	14	7 ₁₁
	15	5 ₁₁ + 1 ring of 4
	16	<i>n</i> = 7
	17	5 ₁₁ + 1 ring of 4
	18	5 ₁₁ + 1 ring of 4
Texas		
Brewster Co.	Anderson 3030	5 ₁₁ + 1 ring of 4
Presidio Co.	Munz & Gregory 23389	7 ₁₁ (G)
Upton Co.	Raven & Gregory 19240	7 ₁₁ (4 plants)

^a All collection numbers and chromosomal determinations are my own unless annotated as follows: (G) = Gregory & Klein, 1960; (R) = Raven, unpublished; (K) = Kurabayashi et al., 1962; (L) = Lewis et al., 1958; (H) = Hagen, 1950; (L & B) = Linder & Brun, 1957.

^b No voucher specimen seen; identity uncertain.

ment. Numbers of extra, diminutive chromosomes ranged from 1 to 11, but the numbers were highly variable within populations and seemed to vary even among separate determinations from a single plant. The extra, diminutive chromosomes of *Calylophus* differed from those reported in *Gaura* (Gregory & Klein, 1960) and in *Oenothera* (Cleland, 1951, 1967; Cleland & Hyde, 1963) in often being heteropycnotic; pairing of the diminutive, extra chromosomes was frequent in all three genera of Onagraceae. The extra, diminutive chromosomes reported by Östergren (1947) in *Anthoxanthum* were heteropycnotic like those in *Calylophus*. Cleland (1951, 1967; Cleland & Hyde, 1963) has hypothesized that the extra, diminutive chromosomes in *Oenothera hookeri* Torr. & A. Gray, may have been derived following hybridization between this species of *Oenothera* and an entity belonging to another group of the genus. This appears doubtful since it has not been demonstrated that the chromosomes of the different groups of *Oenothera* differ significantly in size, or that their differences are or would be maintained in hybrids. Certainly, it would be very difficult to construct an analogous hypothesis for similar chromosomes in *Calylophus* and *Gaura*.

In *Calylophus*, supernumerary chromosomes of normal morphology were found only in one population of *C. berlandieri* subsp. *berlandieri* (Towner 140), in which plants had one to two extra chromosomes. These resembled supernumeraries as found in *Clarkia* (Lewis 1951; Håkansson, 1949), *Camissonia* (Raven, 1962), *Gaura* (Gregory & Klein, 1960; Raven & Gregory, 1972b), and *Gayophytum* (Lewis et al., 1958).

Inversion differences were encountered only in some experimental hybrids between *C. berlandieri* subsp. *berlandieri* and *pinifolius*, and also in some crosses between *C. hartwegii* and *C. lavandulifolius*. No evidence of inversion heterozygosity in natural populations was obtained, but it could well occur as an infrequent event.

Chromosomal determinations from experimental hybrids indicated that the taxa within sect. *Salpingia* have become differentiated by no more than 3 reciprocal translocations and, rarely, by an inversion. Among *C. tubicula* and all subspecies of *C. hartwegii*, crosses showed either complete homology or 1 to 2 translocation differences. *Calylophus lavandulifolius* differed from the above by 2 to 3 translocations and an inversion. The two subspecies of *C. berlandieri*, on the other hand, have become strongly differentiated, based on the current evidence. Hybrids between them were heterozygous for 2–6 translocations and sometimes for 1 inversion. Moreover, geographically separated populations of *C. berlandieri* subsp. *berlandieri* showed differences of the same magnitude. Reciprocal crosses of *C. serrulatus* and *C. berlandieri* produced hybrids with 3–6 translocation differences. Lastly, the few determinations from intersectional hybrids between *C. tubicula* and *C. berlandieri* demonstrated differences of at least 5 translocations. In the hybrid plants meiotic chromosome pairing was variable and poor, while anaphase movement was irregular. The high degree of sterility seen in these and other intersectional hybrids was probably derived from such chromosomal causes. In contrast, hybrid pollen fertility was moderate to high for most intrasectional crosses. Lower hybrid fertility in certain intra-

TABLE 2. *Calylophus* populations examined for self-incompatibility.^a

Taxon	Locality	Collection	Results
<i>C. hartwegii</i> subsp. <i>hartwegii</i>	Chihuahua, Mexico	Breedlove 14305	SI
	Zacatecas, Mexico	Breedlove 14344	SI
	Zacatecas, Mexico	Breedlove 15485	SI
<i>C. hartwegii</i> subsp. <i>maccartii</i>	Durango, Mexico	Breedlove 14305A	SI
	Aguascalientes, Mexico	McVaugh 16680	SI
	Kinney Co., Texas	Strother 299	SI
	San Patricio Co., Texas	Raven & Gregory 19386	SI
<i>C. hartwegii</i> subsp. <i>filifolius</i>	Zapata Co., Texas	Perez 42	SI
	Otero Co., New Mexico	Munz & Gregory 23335	SI
	Ward Co., Texas	Raven & Gregory 19159	SI
	Winkler Co., Texas	Irving 69	SI
<i>C. hartwegii</i> subsp. <i>fendleri</i>	Apache Co., Arizona	Towner 112	SI
	Presidio Co., Texas	Jackson in 1964	SI
<i>C. hartwegii</i> subsp. <i>pubescens</i>	Irion Co., Texas	Raven & Gregory 19211	SI
	Pecos Co., Texas	Munz & Gregory 23405	SI
	Terrell Co., Texas	Gregory 275	SI
<i>C. lavandulifolius</i>	White Pine Co., Nevada	Anderson 2897	SI
<i>C. toumeyii</i>	Cochise Co., Arizona	Towner 107	SI
<i>C. tubicula</i> subsp. <i>tubicula</i>	Brewster Co., Texas	Anderson 3030	SI
	Upton Co., Texas	Raven & Gregory 19240	SI
<i>C. tubicula</i> subsp. <i>strigosus</i>	Nuevo León, Mexico	U. of Kansas Exped. 119	SI
	Hartley Co., Texas	Roberts 35	SI
<i>C. berlandieri</i> subsp. <i>berlandieri</i>	Hemphill Co., Texas	Delso 122	SI
	Lipscomb Co., Texas	Rowell 10414	SI
<i>C. berlandieri</i> subsp. <i>pinifolius</i>	Victoria Co., Texas	Bohart & Thorp 650928-1	SI
	Hays Co., Texas	Raven & Gregory 19368	SI
	Menard Co., Texas	Raven & Gregory 19273	SI
<i>C. serrulatus</i>	Comanche Co., Oklahoma	Anderson 2416	SC
	Aransas Co., Texas	Raven & Gregory 19393	SC
	Cameron Co., Texas	Towner 187	SC
	San Patricio Co., Texas	Towner 184	SC

^a In most cases, tests for self-incompatibility were performed on plants grown from field-collected seed.

sectional crosses involving *C. lavandulifolius* and some involving *C. berlandieri* was correlated with cytological differences between the parental plants.

FLORAL BIOLOGY AND POLLINATION

Information on floral biology is based on the field work of D. P. Gregory (1964 and personal communication) and P. H. Raven (personal communication), and on my own field work and study of cultivated plants. Collections of flower visiting insects were made, and these are to be deposited at the California Insect Survey, Berkeley. Determination of ultraviolet reflection and absorption patterns was carried out by photography with black and white film under near-ultraviolet illumination. All taxa of *Calylophus* were tested for self-incompatibility by making repeated attempts at self-pollination. Table 2 lists those populations which were tested.

The breeding systems of *Calylophus* are of three basic types. That of *C. serrulatus* is based on complex structural heterozygosity. In this species the flowers are highly autogamous, often self-pollinating before anthesis (Fig. 6). For this system insect visitation and pollen transfer are unnecessary, and are in fact uncommon in *C. serrulatus*. The other two types of systems involve self-sterility and insect pollination.

In sect. *Salpingia*, with the exception of *C. tubicula*, flowers are adapted for vespertine pollination by hawkmoths. They have narrow floral tubes measuring 25–50 mm in length (Figs. 1–3), sweet-scented nectar, large exerted stigmas, vespertine or afternoon anthesis, and, except for *C. toumeyi*, strongly ultraviolet-reflective areas on the distal portions of the petals (Figs. 7, 10). These reflective areas on the petals contrast markedly with small ultraviolet-absorptive regions which are usually present in the center of the flower. Populations of the tubular-flowered taxa experience vespertine and nocturnal visitation by hawkmoths, especially the abundant and effective pollen vector *Hyles lineata* (Fabr.) (*Celerio lineata*). Some taxa and populations within taxa of *C. hartwegii* tend to have mid-afternoon anthesis and large- to moderate-sized ultraviolet-absorptive areas in the center of the flower. These seem to be secondary adaptations for bee pollination. Many populations of taxa in sect. *Salpingia* are visited in the afternoon, early evening, and even morning by halictid, anthophorid, and other bees. Some of these are oligolectic for the Onagraceae and probably contribute to pollination. The late-opening subspecies of *C. hartwegii* (Figs. 9, 10), along with *C. lavandulifolius* and *C. toumeyi*, have ultraviolet patterns less appropriate for bee pollination. The last species has no strongly ultraviolet-reflective areas on the petals (Figs. 11, 12). In these taxa bee visitation is restricted to the early evening and is probably less effective in pollination.

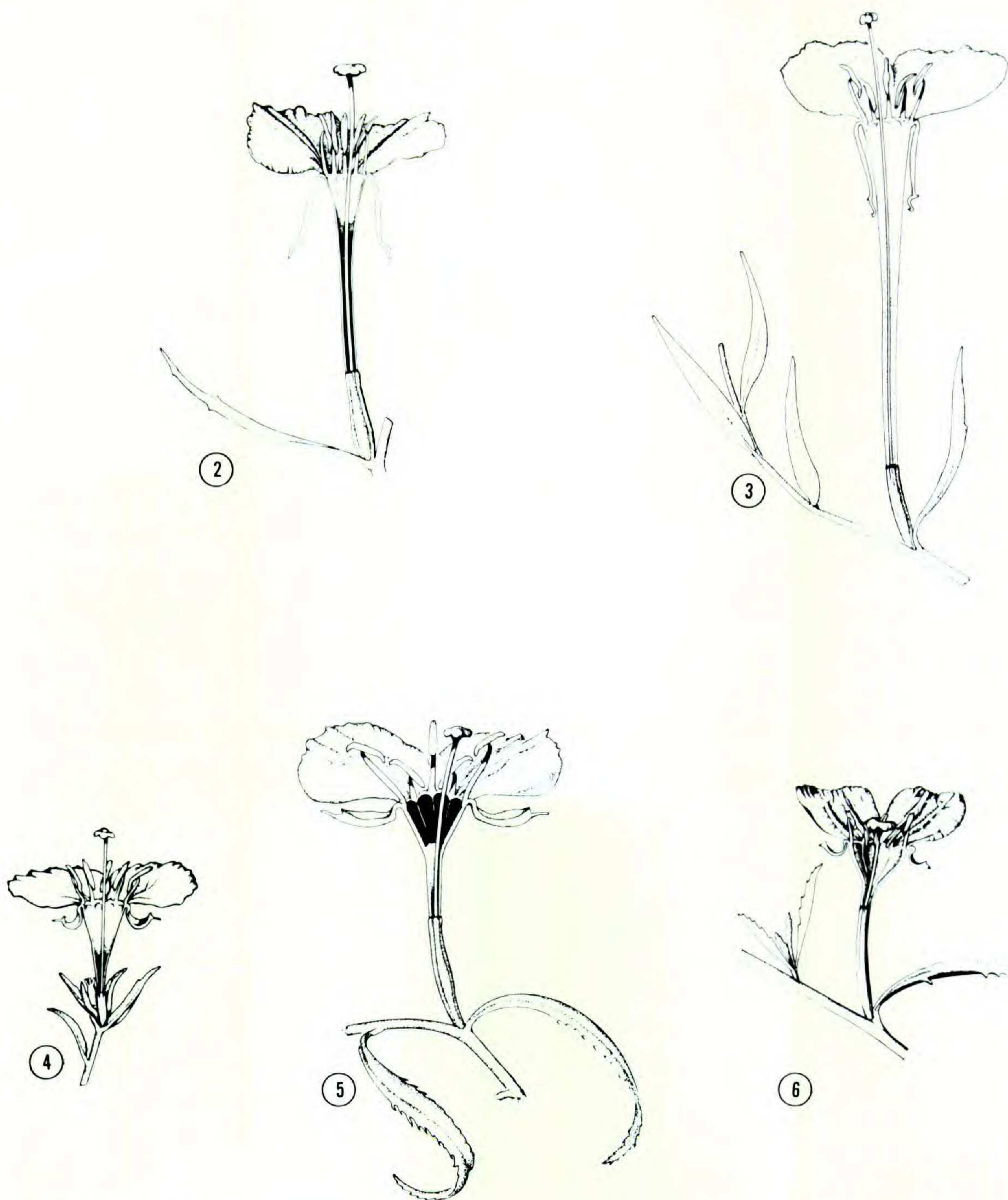
Calylophus tubicula and *C. berlandieri* are pollinated by matinal and diurnal insects. Their flowers open in the early morning, have short funnelform tubes (Figs. 4, 5), and display large ultraviolet-absorptive regions in their centers (Figs. 13, 14). The petals are highly ultraviolet-reflective distally. Based on the available evidence, the primary insect visitors to *C. tubicula* seem to be morning-active halictid bees. Other potential pollinators include hawkmoths, which visit the flowers lightly at about sunrise.



FIGURE 1. *Calylophus toumeyii* in the Chiricahua Mountains, Cochise Co., Arizona (Towner 107).

A great variety of insects come to the flowers of *C. berlandieri*, which appears to possess a generalized pollination system. Beetles, skippers, small butterflies, occasional hawkmoths, and a wide variety of bees have been observed gathering pollen or nectar. Each of these groups may contribute to pollination, with its relative importance varying with locality.

When present, ultraviolet patterns on the flowers serve to direct insects to the anthers and nectar. The pattern typical of *Calylophus* consists of absorptive regions at the base of the petals, at the mouth of the floral tube, and on the stigma and anthers (Figs. 8, 10, 14). *Calylophus toumeyii* differs in having moderate ultraviolet absorption over the entire flower (Fig. 12). In Onagraceae, ultraviolet absorption results from the presence of one or more flavonoids with absorption maxima in the near-ultraviolet (Dement & Raven, 1973, 1974). As in many other yellow-flowered Onagraceae, the ultraviolet-absorptive portions of the petals of *Calylophus hartwegii* and *C. serrulatus*, and presumably those of the other species as well, contain isosalipurposide, a chalcone with an absorption maximum at 365 m μ (Dement & Raven, 1973, 1974, and personal communication). In addition, *C. hartwegii* has an accompanying flavonol, myrecetin-3-glucoside or galactoside, and *C. serrulatus* has an unidentified compound that resembles an aurone, a class of flavonoid that is frequently associated with chalcones in Asteraceae (W. Dement, personal communication). All of these flavonoids are absent from the ultraviolet-reflective portions of the petals. Carotenoids absorbing maximally at 400–470 m μ are found throughout the petals.



FIGURES 2-6. Longitudinal sections of flowers of *Calylophus*.—2. *C. hartwegii* subsp. *hartwegii*.—3. *C. toumeyii*.—4. *C. tubicula* subsp. *tubicula*.—5. *C. berlandieri* subsp. *pinifolius*.—6. *C. serrulatus*. All $\times 1.1$.

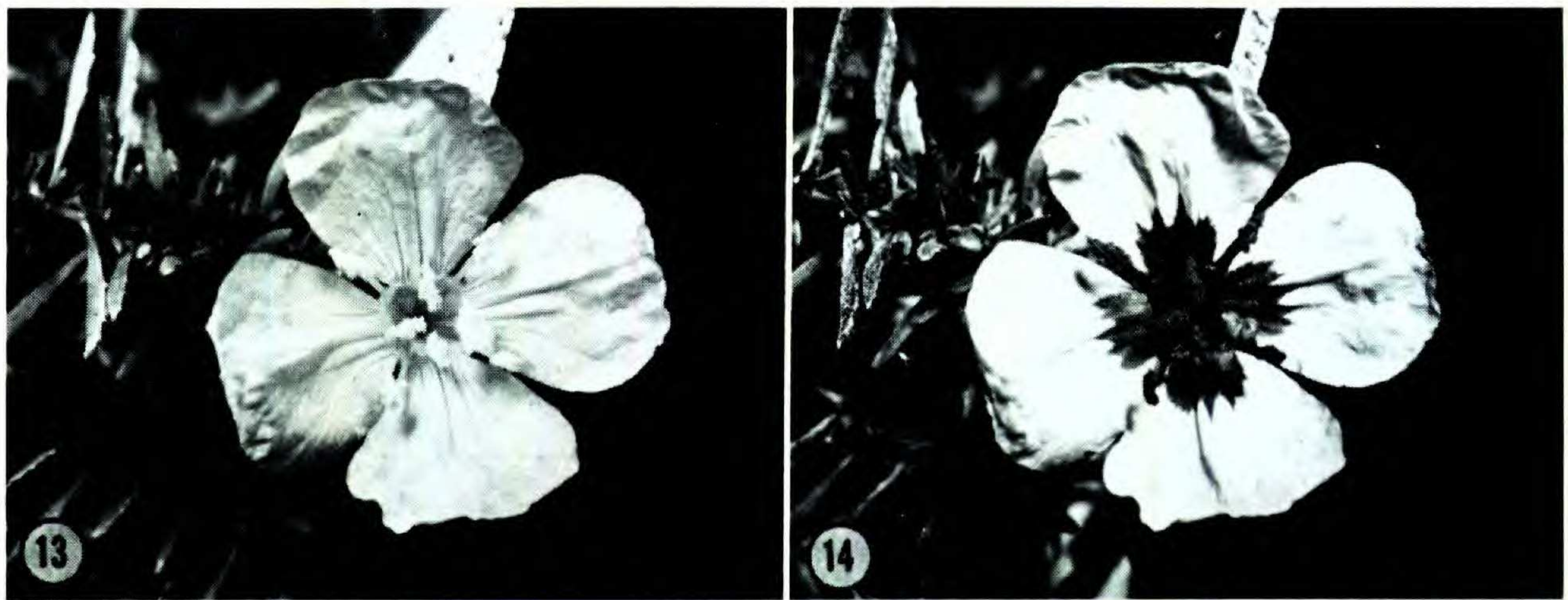
Therefore, insects with trichromatic vision would see the petal apex color as "bee yellow" and the petal base, anthers, and stigma as "bee purple."

It is uncertain whether these ultraviolet patterns would be as effective for hawkmoth pollination after sunset as they are for diurnal insects in sunlight. The small size or absence of ultraviolet absorbing areas in the evening-opening *Calylophus* perhaps signifies that such patterns are not useful for insect orientation at night. Alternatively the minimization of ultraviolet contrast patterns may have evolved to lessen pollen and nectar removal by diurnal insects inefficient in pollinating the vespertine *Calylophus*. This could be especially true in the



FIGURES 7-12. Flowers of *Calylophus* under fluorescent and ultraviolet illumination. Collections refer to seed sources.—7. *C. hartwegii* subsp. *hartwegii* (Durango, Mexico, *Breedlove 14305A*); fluorescent illumination, emasculated.—8. Same, with ultraviolet illumination.—9. *C. hartwegii* subsp. *fendleri* (Presidio Co., Texas, *Jackson in 1964*); fluorescent illumination.—10. Same, with ultraviolet illumination.—11. *C. toumeyi* (Cochise Co., Arizona, *Towner 107*); fluorescent illumination.—12. Same, with ultraviolet illumination.

case of *C. toumeyi*, which has flowers contrasting only slightly with its vegetative parts and the background in the ultraviolet region of the spectrum. Mazokhin-Porshnyakov (1969) states that considerable ultraviolet light is present at night, especially in moonlight. However, the moths investigated have shown low sensitivities to ultraviolet light, and become functionally colorblind at light levels below 0.05 lux. Their maximum sensitivity to light is in the yellow to green



FIGURES 13–14. Flowers of *Calylophus berlandieri* subsp. *berlandieri* (Hartley Co., Texas, Roberts 35) under fluorescent and ultraviolet illumination.—13. Fluorescent illumination.—14. Ultraviolet illumination.

region of the spectrum. If hawkmoths follow this pattern, they could locate *Calylophus* flowers merely by their scent and reflectivity at wavelengths greater than $480\text{ m}\mu$, eliminating any need for ultraviolet reflection. With the moderate light levels present at dusk both bees and moths could probably utilize the ultraviolet contrast patterns for orientation.

PHYLOGENETIC RELATIONSHIPS

The species of *Calylophus* fall into two clearly recognizable but related groups. Those with keeled sepals and two sets of stamens of unequal length are included in sect. *Calylophus* and those with plane sepals and subequal stamens are assigned to sect. *Salpingia*. No intermediates between these sections have been found, and the species of the two groups are intersterile while being relatively infertile among themselves. Fifty-one of 101 intersectional crosses yielded some seed, with the amount set ranging from 5 to 81% of normal, but germination was poor (1–3%) and the few weak hybrids that grew to maturity were largely sterile (0–10% pollen fertility). Members of sect. *Salpingia* are most likely primitive in comparison with those of sect. *Calylophus*, as they have a clumped perennial habit and, except for *C. tubicula*, are primarily pollinated by hawkmoths. In growth form, the members of sect. *Salpingia* resemble the more generalized forms of *Gaura* (Raven & Gregory, 1972a), a genus which is also primarily moth-pollinated and closely related to *Calylophus*.

Among the hawkmoth-pollinated members of sect. *Salpingia*, *C. lavandulifolius* seems to be the most distinct, having a more caespitose habit than the other forms and a broad geographical distribution which includes numerous relict populations. *Calylophus toumeyii* appears to be most closely related to the southern subspecies of *C. hartwegii*, especially *C. hartwegii* subsp. *hartwegii*, with which it shares long free sepal tips, preference for montane habitats, and strigulose pubescence. Within *C. hartwegii* a pattern of reticulate relationships is evident and relative affinities are difficult to assess. *Calylophus hartwegii* subsp. *maccartii*, occupying the Texas coastal plain, is likely a recent derivative of

C. hartwegii subsp. *hartwegii*, as these two forms share several characters and are geographically adjacent. *Calylophus hartwegii* subsp. *pubescens*, *C. hartwegii* subsp. *fendleri*, and *C. hartwegii* subsp. *filifolius* seem to constitute a series of related forms occupying slightly different ecological zones in the plains of the southwestern United States. The subspecies of *C. hartwegii* are connected by zones of intergradation, although not all of the possibilities for geographical contact and gene exchange are realized. The short-lived perennial *C. tubicula* is unique in sect. *Salpingia*, having several characteristics of bee-pollinated flowers. It is likely a specialized derivative of relatively recent origin.

Sect. *Calylophus* is apparently more specialized in having an annual or short-lived perennial habit, and perhaps also in its adaptations to diurnal pollination. Of the two species in the section, *C. berlandieri* is clearly the more generalized, having a self-incompatibility system, and chromosomes which form bivalents or small rings at meiotic metaphase I. *Calylophus serrulatus*, a highly autogamous complex structural heterozygote, is a specialized offshoot of either the former species or a common ancestor. No clear knowledge of the exact ancestry of *C. serrulatus* is available, although hypothetical lineages have been worked out for some of the other complex heterozygotes in the Onagraceae. It may be that this species developed through the independent origin of complex structural heterozygosity in different geographic regions. This is suggested by the fact that neighboring populations of *C. serrulatus* and *C. berlandieri* often tend to resemble one another phenetically, a condition which could be attributable to multiple ancestry for *C. serrulatus*, to introgressive genetic exchange, or to parallel responses by the two species to local selective regimes. *Calylophus serrulatus* is highly successful and widespread in the Great Plains from Canada to New Mexico and also occurs in Arizona and Mexico. *Calylophus berlandieri* is largely restricted to Texas.

A likely but speculative evolutionary sequence could have begun with the primary divergence of the ancestors of the two sections. Accompanying this split was the development of morning anthesis and other characteristics of day-pollinated flowers in sect. *Calylophus*. The moth-pollinated perennial ancestors of sect. *Salpingia* probably evolved more slowly, but gave rise to *C. tubicula*. *Calylophus serrulatus* presumably developed very recently from *C. berlandieri* or its ancestors. The course of evolution within sect. *Salpingia* seems to have depended upon ecogeographical differentiation among the various forms, while being little dependent on cytological transformations. Cyclic climatic fluctuations in Pleistocene and Recent times have undoubtedly contributed to the taxonomic differentiation within sect. *Salpingia*, judging from the confusing patterns of overlapping geographical ranges, isolated populations, and introgression that are now in evidence among its taxa.

Divergence within sect. *Calylophus* has been marked by much greater cytological change than in sect. *Salpingia*. Several chromosomal rearrangements involving translocations were required for the derivation of *C. serrulatus* from pair-forming outcrossers. Similar chromosomal repatterning has also occurred within *C. berlandieri*, and characterizes at least three series of populations. In addition, the two races of *C. berlandieri* appear to be ecologically differentiated,

and remain well separated in regions where there exists a discontinuity between their respective habitats.

TAXONOMY

Calylophus Spach, Hist. Nat. Vég. Phan. 4: 349. 1835.

"*Calylophis*" Spach, Nouv. Ann. Mus. Hist. Nat. 4: 337. 1835.

Meriolix Raf. ex Endl., Gen. Pl. 1190. June 1840; Raf., Amer. Monthly Mag. & Crit. Rev. 4: 192. 1819, nom. nud.; Raf., J. Phys. Chim. Hist. Nat. Arts 89: 259. 1819, nom. nud.

TYPE: *Meriolix serrulata* (Nutt.) Walp. = *Calylophus serrulatus* (Nutt.) Raven.

Salpingia (Torr. & A. Gray) Raim. in Engler & Prantl, Natürl. Pflanzenfam. 3(7): 217. 1893.

Based on *Oenothera* subg. *Salpingia* Torr. & A. Gray, Fl. N. Amer. 1: 501. 1840. TYPE: *Oenothera lavandulaefolia* Torr. & A. Gray = *Calylophus lavandulifolius* (Torr. & A. Gray) Raven.

Galpinsia Britton, Mem. Torrey Bot. Club 5: 236. 1894. Based on *Oenothera* subg. *Salpingia* Torr. & A. Gray, Fl. N. Amer. 1: 501. 1840. TYPE: *Galpinsia hartwegii* (Benth.) Britton = *Calylophus hartwegii* (Benth.) Raven.

Herbaceous to suffrutescent perennials, rarely annual, from a woody caudex, flowering in the first year. Stems nearly prostrate or decumbent to erect, with grey to pinkish brown epidermis, this sometimes exfoliating. No basal rosette, leaves cauline, more or less sessile, alternate, entire to spinuose-serrate, the upper leaves more or less uniform in size, the lowermost often somewhat larger; stipules absent. Flower 4-merous, actinomorphic, borne in the axils of the upper leaves, opening in the early morning or from midafternoon to near sunset, with the stigma receptive and anthers shedding pollen simultaneously upon anthesis or soon afterwards, wilting in 1½ to 2 days; buds erect in inflorescence. Floral tube well developed and prolonged beyond the ovary, deciduous after anthesis. Sepals greenish yellow, often with purple or red markings, reflexed separately. Petals yellow, in some species becoming red, orange, or purple upon wilting, reflexed in anthesis. Style yellow; stigma yellow to yellow green, occasionally blue black in one species, peltate, discoid to nearly square, sometimes obscurely and shallowly 4-lobed. Stamens 8, yellow; anthers narrowly elliptic to linear, versatile, the sporogenous tissue divided into packets within each locule; pollen yellow, shed singly. Capsule many seeded, sessile, cylindrical, and often narrowed at each end, obtusely 4-angled, longitudinally dehiscent, persisting on the stem after dehiscence. Seeds in 2 rows in each of the 4 locules. Basic chromosome number, $x = 7$. Five of the six species are self-incompatible.

TYPE SPECIES: *Calylophus nuttallii* Spach = *C. serrulatus* (Nutt.) Raven.

In the accounts which follow, the taxa will be grouped according to their phenetic affinities. Specimens cited were selected to represent the ranges of morphological variation and geographical occurrence. Where possible, I gave preference to recent collections and those with numbers of duplicates. My own collections are deposited in the Dudley Herbarium of Stanford University (DS) with duplicates to be distributed.

KEY TO SECTIONS

- a. Sepals plane, lacking a keeled midrib; stamens subequal Section I. *Salpingia*
 aa. Sepals with conspicuously keeled midrib; stamens biseriate, the episepalous filaments about twice as long as the epipetalous filaments Section II. *Calylophus*

KEY TO SPECIES

Section I. *Salpingia*

- a. Floral tube funnellform in the upper two-thirds or more, or less than 15 mm long; flowers opening near sunrise 4. *C. tubicula*
- aa. Floral tube funnellform in upper half or less, 15–55 mm long; flowers opening near sunset.
- b. With conspicuous axillary fascicles of small leaves, these up to 30 mm long; subulate sepal tips 2–9(–12) mm long; capsule thin walled and dehiscent only in the distal portion; montane distribution, northwestern Mexico to southeastern Arizona 3. *C. toumeyii*
- bb. With or without axillary fascicles of leaves or if present, these less than 20 mm long; subulate sepal tips 0.5–6 mm long; capsule thicker walled, dehiscent along its entire length.
- c. Plants low, frequently caespitose, mostly 0.4–2 dm high; densely gray-strigulose; sepal tips short, 0.3–3 mm long 2. *C. lavandulifolius*
- cc. Plants not caespitose, mostly taller and more openly branched, 0.4–4 dm high; variously pubescent or glabrous; if strigulose, sepal tips 2–6 mm long 1. *C. hartwegii*

Section II. *Calylophus*

- a. Flowers small, the petals mostly 5–12 mm long; stigma positioned near the apex of the floral tube or slightly beyond, within the circle of anthers; 30–80% of pollen grains aborted 6. *C. serrulatus*
- aa. Flowers usually larger, the petals mostly 9–25 mm long; stigma well exerted, usually to the end of the episepalous anthers or beyond; 85–100% of pollen grains fertile 5. *C. berlandieri*

Section I. *Salpingia* (Torr. & A. Gray) Towner, comb. nov.

Oenothera subgen. *Salpingia* Torr. & A. Gray, Fl. N. Amer. 1: 501. 1840. *Salpingia* (Torr. & A. Gray) Raim. in Engler & Prantl, Natürl. Pflanzenfam. 3(7): 217. 1893. *Galpinsia* Britton, Mem. Torrey Bot. Club 5: 236. 1894.

Herbaceous to suffrutescent perennials 0.4–6 dm high, glabrous to glandular-pubescent, strigulose, or with spreading trichomes. Leaves 0.3–5 cm long, entire to serrulate. Inflorescence sparse to dense; buds terete. Flowers opening in afternoon, evening, or morning. Floral tube terete, tubular and gradually expanded through its entire length, or tubular proximally and funnellform distally, 5–70 mm long. Sepals plane. Petals suborbicular to rhomboidal or squarish. Stamens nearly equal in length. Capsule promptly dehiscent upon drying, usually not curved.

TYPE SPECIES: *Calylophus lavandulifolius* (Torr. & A. Gray) Raven.

1. *Calylophus hartwegii* (Benth.) Raven, Brittonia 16: 286. 1964.

Oenothera hartwegii Benth., Pl. Hartw. 5. 1839.

Herbaceous to suffrutescent perennial arising from a woody caudex; stems one to many, sparingly to densely branched above, nearly prostrate to erect, 0.4–5 dm high, strigulose, glandular-pubescent, glabrous, or with spreading hairs, more densely pubescent above. Leaves sparsely to densely distributed along the stem, sessile or indistinctly petiolate, spreading to ascending, sometimes reflexed, linear or filiform to ovate or oblanceolate, 3–50 mm long, 0.4–12 mm wide, usually not much reduced up to the stem, variously pubescent or glabrous, the tip acute

to obtuse, the base acute-attenuate to truncate-clasping, the margin entire to serrate, frequently undulate; fascicles of small leaves 1–15 mm long sometimes present in the nonfloriferous axils; lowest stem leaves sometimes wider than above, frequently obovate to spatulate, to 65 mm long. Inflorescence lax, with rarely more than one flower at a time fresh on a stem, variously pubescent or glabrous; buds terete. Floral tube terete, tubular in the lower one-half or more, gradually expanded distally, 16–50(–60) mm long, 4–20 mm wide at the throat of pressed specimens, variously pubescent or glabrous without, the inner surface glabrous distally, sometimes minutely pubescent at the base, frequently fading to pink or purple on wilting. Sepals 7–28 mm long, 2–10 mm wide, with subulate free tips 0.5–6 mm long, plane, variously pubescent or glabrous, pale yellow-green, frequently with purple spotting or marginal stripes, fading as with the floral tube. Petals suborbicular to rhomboidal, 10–35 mm long, similar in width, highly ultraviolet-reflective, with basal ultraviolet-absorptive spot of varying size, sometimes absent, frequently turning pinkish or purplish upon wilting. Stamens subequal; filaments 4–13 mm long, glabrous; anthers 5–13 mm long. Style 25–65 (–75) mm long, usually exceeding the stamens, minutely pubescent below; stigma flat to slightly revolute, squarish, 1.5–6 mm broad; ovary 4–30 mm long, 1–3 mm wide, variously pubescent or glabrous. Capsule 6–40 mm long, 2–4 mm wide, moderately thick-walled, completely dehiscent, straight or slightly curved; seeds 1–2.5 mm long, obovoid, rounded or sharply angled, truncate at the apex. Self-incompatible. Gametic chromosome numbers, $n = 7, 14$.

TYPE: MEXICO. AGUASCALIENTES: Aguascalientes, 1837, *Theodor Hartweg* 10 (K, holotype; P, isotype).

Distribution: Local and colonial to abundant and widespread on rocky, sandy, gypsum, or limestone soils in arid to relatively mesic open areas, in southeastern Colorado, southwestern Kansas, western Oklahoma, Texas (except eastern part), New Mexico, southeastern and east-central Arizona, and in Mexico from Chihuahua, northern Coahuila, and northwestern Tamaulipas south to Aguascalientes. From ca. 30 to ca. 2,500 m elevation. Flowers February to October.

As treated here, *Calylophus hartwegii* includes five intergrading subspecies. The species is distributed over much of the Southwest and northern Mexico, occupying relatively dry plains and mountain regions.

Long, slender floral tubes and vespertine anthesis characterize all subspecies of *C. hartwegii*, suggesting a basic adaptation to hawkmoth pollination. Variation among the subspecies in exact time of anthesis, in ultraviolet reflection patterns, and in flower size was observed, and is likely due to modal differences in pollination systems. Principal flower visitors included halictid and anthophorid bees and hawkmoths, but with differing proportions of these insects visiting the various populations observed. The mean length of the floral tube in this species and in *C. lavandulifolius* and *C. toumeyii* is about 30–40 mm. Anthers and stigma are well exerted beyond the tube, but tend to block the entrance to it. Short-tongued hawkmoths, such as the abundant species *Hyles lineata*

(*Celerio lineata*), land on the flower and extend their heads into the tube to obtain nectar. In doing this they pick up quantities of pollen on the head and thorax and can serve as effective agents of pollination. All subspecies of *C. hartwegii* have been tested at least once for self-incompatibility. In a brief check, each of 22 plants examined was found to be self-sterile.

Of 88 diploid plants from 55 populations examined for chromosome configuration, 56 individuals from 42 populations, including some from each subspecies, showed translocation heterozygosity. The mean number of heterozygosities per plant was 1.0 for the species as a whole. Plants with as many as 5 translocation heterozygosities were found in seed obtained from natural populations, but most individuals had only 1 or 2, displaying 1 or 2 rings of 4 chromosomes or a ring of 6 at meiotic metaphase I.

Calylophus hartwegii is a predominantly diploid species, although occasional tetraploids and plants with extra chromosomes were found. Sixteen plants from nine populations, including all subspecies but *C. hartwegii* subsp. *pubescens*, had extra diminutive chromosomes. Five of the 62 populations from which chromosome number determinations have been made contained tetraploid individuals. No population was found to be comprised of both tetraploid and diploid plants, although the low number of duplicate counts from tetraploid populations leaves this possibility open. One plant intermediate between subspp. *pubescens* and *hartwegii* (Towner 3) appeared to be triploid, further increasing this likelihood. Tetraploids were found in *C. hartwegii* subspp. *pubescens*, *hartwegii*, and *macartii*, all predominantly diploid taxa.

Difficulties of interpreting the variation in this species have arisen from a number of causes. The entities in sect. *Salpingia* tend to have extensive geographical ranges which overlap and interdigitate. Minor ecological differences often separate the taxa locally. The subspecies of *C. hartwegii* are distinguished morphologically from one another by a few rather slight differences such as pubescence and leaf shape. The pattern of variation within the section is reticulate, with few characters varying concordantly. Broad areas of introgression exist between certain of the taxa, while others show greater discontinuities in areas of contact. All forms retained in *C. hartwegii* are connected either directly or indirectly by intergradation. The center of the distribution of this species in western Texas and northern Mexico is characterized by an abundance of forms occurring in near proximity and by a complex display of variation.

Absence of any significant number of intermediates in the appropriate regions indicates that *C. hartwegii*, *C. lavandulifolius*, and *C. toumeyii* should be distinguished specifically. The earlier decision to combine them (Towner & Raven, 1970) was intended to emphasize the overall unity of this group, but a subsequent thorough study of herbarium material failed to bring forth evidence of intergradation among the three species.

Populations of *C. hartwegii*, as mentioned above, occasionally occur sympatrically with *C. berlandieri*, *C. serrulatus*, and *C. tubicula*. They also frequently occur mixed with *C. lavandulifolius*, and only rarely form hybrids with that species.

KEY TO SUBSPECIES

- a. Ovary (and usually stems and leaf margins) with spreading trichomes; leaves (except lowest) abruptly narrowed to truncate or slightly clasping at the base; widespread 1e. subsp. *pubescens*
- aa. Plant without spreading trichomes; leaves gradually narrowed at the base or extremely narrow throughout.
 - b. Plant glabrous or nearly so; flowers opening from one hour before to one hour after sunset; widespread 1d. subsp. *fendleri*
 - bb. Plant, especially on ovary and upper stems, with some form of pubescence; flowers usually opening 2–5 hours before sunset, occasionally later.
 - c. Ovary and stems with short glandular pubescence; leaves glabrous to glandular-pubescent, rarely sparsely strigulose, filiform to narrowly lanceolate; gypsum or limestone flats, central New Mexico to northern Mexico 1c. subsp. *filifolius*
 - cc. Ovary, stem, and leaves usually strigulose, or if glandular-pubescent, the the leaves narrowly lanceolate to lanceolate or oblanceolate.
 - d. Leaves mostly 4.5 to 11 times as long as wide, usually with crinkled-undulate margins; plant sparsely strigulose or occasionally minutely glandular-pubescent; low plains from southeastern Texas to northern Mexico 1b. subsp. *maccartii*
 - dd. Leaves mostly 9 to 35 times as long as wide, usually not crinkled; plant sparsely to densely strigulose; high plains and mountains from southern Trans-Pecos Texas to Aguascalientes 1a. subsp. *hartwegii*

1a. ***Calylophus hartwegii*** (Benth.) Raven subsp. ***hartwegii***; Towner in Correll and Johnston, Man. Vasc. Pl. Texas 1121. 1970.—FIG. 2.

Salpingia hartwegii (Benth.) Raim. in Engler & Prantl., Natürl. Pflanzenfam. 3(7): 217. 1893.

Galpinsia hartwegii (Benth.) Britton, Mem. Torrey Bot. Club 5: 236. 1894. *Oenothera hartwegii* Benth. var. *typica* Munz, Amer. J. Bot. 16: 706. 1929, pro parte. *Calylophus hartwegii* var. *hartwegii*; Shinnars, Sida 1: 342. 1964, pro parte. *Oenothera hartwegii* var. *hartwegii*; Munz, N. Amer. Fl., ser. 2, 5: 139. 1965, pro parte.

Oenothera greggii A. Gray var. *pringlei* Munz, Amer. J. Bot. 16: 711. 1929, pro parte. *O. pringlei* (Munz) Munz, N. Amer. Fl., ser. 2, 5: 138. 1965, pro parte. TYPE: Bachimba Canyon, Chihuahua, Mexico, 27 March 1885, C. G. Pringle 224 (GH).

Oenothera lavandulaefolia Torr. & A. Gray var. *typica* Munz sensu Munz, Amer. J. Bot. 16: 704. 1929, pro parte. *O. lavandulifolia* var. *lavandulifolia* sensu Munz, N. Amer. Fl., ser. 2, 5: 138. 1965, pro parte.

Stems several to many, sparingly branched above, decumbent to somewhat ascending, or plant tufted, 0.5–3 dm high; plant grayish-strigulose throughout, more densely so on the ovary and inflorescence than elsewhere. Leaves dense on stems, more or less ascending, linear to narrowly lanceolate, 10–35 mm long, 0.5–4 mm wide, the tip acute, the base acute-attenuate, the margin entire to shallowly and sparsely serrulate, occasionally undulate; fascicles of small leaves 2–15 mm long usually present in the axils. Floral tube (18–)30–50(–60) mm long, 4–13 mm wide at the throat, sometimes with purple longitudinal bands, often fading purplish. Sepals 8–20 mm long, 3–7 mm wide, with free tips (1–)2–6 mm long, frequently with purple marginal stripes. Petals squarish or rhomboidal, 13–30 mm long, frequently fading to a purple or pink color, with basal ultra-violet-absorptive spot absent or present and of small to moderate size. Filaments 5–10 mm long; anthers 5–9 mm long. Style 30–65(–75) mm long, glabrous; stigma 2–5 mm broad; ovary 5–12 mm long, 1–2 mm wide. Capsule 10–25 mm long, 2–4 mm wide; seeds 1–2.5 mm long. Self-incompatible. Gametic chromosome numbers, $n = 7, 14$.



FIGURE 15. Distributions of *Calylophus hartwegii* subsp. *hartwegii* (dots), *C. hartwegii* subsp. *maccartii* (triangles), and intergrades between the two subspecies (open circles).

Distribution (Fig. 15): Mostly on rocky or gravelly soil, sometimes limestone, in rugged canyons in the northern part of the range, to high plains and mountains, reaching pine forest at the southern limits of the range, from Brewster and southern Hudspeth cos., Texas, south through central Chihuahua, Coahuila, western Nuevo León, and eastern Durango to central and southeastern Zacatecas, Aguascalientes, and southwestern San Luis Potosí. Elevational distribution from ca. 900 m (near Solis, Brewster Co., Texas) to at least 2,300 m (6 mi N of Zacatecas, Zacatecas, Mexico). Flowers February to October.

Representative specimens examined:

UNITED STATES. TEXAS: Brewster Co.: Nr. Solis, just N of Mariscal Canyon, Big Bend National Park, *Johnston & Correll* 24568 (LL). Head of Fresno Canyon, Big Bend Ranch, *Correll & Rollins* 23672 (LL). Near Marathon, *Young* 174 (MO, TEX). Hudspeth Co.: Panther Hill-Fox Hill area of the central Malone Mts., *Waterfall* 5830 (GH, NY). Val Verde Co.(?): Pecos R., *Thurber* 123 (NY). County unknown: Coyote Mt., West Texas, *Havard* 37704 (CAN).

MEXICO. CHIHUAHUA: 12 mi W of General Trias, *Breedlove* 15741 (DS). 5 mi S of Hidalgo del Parral, *Breedlove* 15745 (DS). 13 mi E of Hidalgo del Parral, *Breedlove* 14305 (DS). Santa Eulalia Mts., *Rose* 11693 (US). Santa Eulalia Hills, *Wilkinson* 4601 (F, NY). Ca. 30 mi NW of Chihuahua, *Lee* 59 (F, TEX). Vicinity of Chihuahua, *Palmer* 59 (F, MO, NY, US). Alberto, SE of Chihuahua, *Pennell* 18627 (NY, PH, US). 11 mi N of Parral, *Waterfall* 12514 (OKLA). Chihuahua, *Le Sueur* 130 (F, UC). Between Parral and Villa Ocampo, *Weber & Charette* 11710 (COLO). Gallego Springs (between Carrizal and Chihuahua), *Wislizenius in* 1846 (MO). Near Chihuahua, *Pringle in* 1886 (F, MO, NY, US). 13 mi N of Ciudad Chihuahua, *Breedlove* 15736 (DS). 24 mi W and 1 S of Chihuahua, *Stuessy* 1020 (TEX). 23 mi W of Chihuahua, *White* 2470 (ARIZ). Near Chihuahua, *Le Sueur* 811 = 58 (F, MO, SMU, TEX, US). COAHUILA: Múzquiz, Palm Canyon, *Marsh* 1002 (F, OKLA, TEX). Múzquiz, *Marsh* 1134 (F, OKLA, SMU, TEX). Cerro de los Árboles, *Jermey* 147 (US). 11 km NE of Jimulco, *Stanford et al.* 9 (ARIZ, DS, MO, NY, UC, WTU). 24 km NW of Fraile, *Stanford et al.* 402 (ARIZ, DS, MO, NY, WTU). Sierra Mojada Mts., *Jones* 233 (MO, POM, US). Sierra Mojada, *Jones in* 1891 (POM). Near Patos (now General Cepeda), *Gregg* 723 (MO). Near Buena Vista, SW of Saltillo, *Gregg* 387 (MO). Ciénega Grande (just NE of Parras), *Gregg* 492 (MO). Allende, *Marsh* 1776 (F, TEX). Sierra de la Paila, *Purpus* 4977 (F, US). Sierra de Parras, *Purpus in* 1905 (UC). Saltillo, *Arsène* 6510 (US). Paso del Diamante, near Saltillo, *Munz* 15034 (MO, POM). 30 mi W of Saltillo, *Wislizenius* 298 (MO). Saltillo (?), *Palmer* 344 (US). Saltillo, *Palmer* 337 (US). 9 mi S of Saltillo, *Straw & Forman* 1337 (RSA). Ca. 20 mi E of Saltillo, *McVaugh* 12301 (RSA). Saltillo, *Fisher* 32 (F, UC). NUEVO LEÓN: 12 mi N of Sabinas Hidalgo, *Heard & Barkley* 14535 (TEX). 4 mi S of Galeana, *McGregor et al.* 65 (DS, KANU, SMU). DURANGO: 46 mi N of La Zarca, *Straw & Forman* 1525 (RSA). 15 km NE of Guadalupe Victoria, *Henrickson* 1762 (DS). 77 mi S of Parral, *Wiens* 3464 (COLO, DS). 6 mi NE of Hidalgo del Parral, *Breedlove* 5947 (DS). 21 mi N of La Zarca, *Breedlove* 14305A (DS). 71 mi NE of Durango, *Waterfall* 13336a (OKLA, RSA, SMU). 3-6 mi W of La Zarca, *Straw & Forman* 1717 (RSA, UC). Ca. 54 mi S of Villa Matamoros, Chihuahua, *Straw & Forman* 2058 (RSA, UC). ZACATECAS: On route 49, 2 km N of Route 45, *Cruden* 1238 (DS). Near Concepción del Oro, *Palmer* 271 (F, MO, NY, UC, US). Gypsum flats, Sierra Hermosa, *Shreve* 8594 (ARIZ). 2 mi SE of Sombrero (Sombrerete?), *Waterfall* 13799 (OKLA, RSA, SMU). 7 mi S of Fresnillo, *Breedlove* 15485 (DS). 9 mi N of Fresnillo, *Breedlove* 15486 (DS). 2 mi SW of Sain Alto, *Breedlove* 5952 (DS). 6 mi N of Zacatecas, *Breedlove* 15481 (DS). 21 mi N of Sombrerete, *Breedlove* 14338 (DS). 27 mi N of Fresnillo, *Breedlove* 14344 (DS). Concepción del Oro, *Pennell* 17416 (PH). "Gravelly soil," *Purpus in* 1903 (UC). Ca. 22 mi NE of Zacatecas, *Straw & Forman* 1492 (RSA). 55 mi W of Zacatecas, *Reveal et al.* 2660 (DS). SAN LUIS POTOSÍ: 8 km NE of Laguna Seca, on km 20 of road from San Luis Potosí to Antiguo Morelos, *Rzedowski* 6325A (RSA). Charcas, *Whiting* 898 (ARIZ). Ca. 5 km NNE of Matehuala, *Rzedowski* 9186 (DS). 44 mi NW of San Luis Potosí on road from Zacatecas, *Breedlove* 5954 (DS). 13 mi NW of San Luis Potosí on road to Zacatecas, *Breedlove* 14346 (DS). 27 mi NW of San Luis Potosí along road to Zacatecas, *Breedlove* 15473 (DS). Charcas, *Lundell* 5125 (ARIZ, DS, F, POM, UC, US). AGUASCALIENTES: 9 mi E of Aguascalientes, *McVaugh* 16680 (RSA, TEX). JALISCO(?): Lake Chapala (locality almost certainly in error) *Lemmon & Lemmon in* 1905 (UC).

Calylophus hartwegii subsp. *hartwegii* occupies a diversity of habitats, including desert scrub, thorn scrub, and pine forest. Typical material for this subspecies comes primarily from montane areas of north-central Mexico, while collections from lower altitudes and more northern localities exhibit evidence of hybridization with other taxa. Poor sampling in the remoter areas of northern Mexico has left details of the geographical range unclear. For example, the occurrence of this subspecies throughout most of northern Coahuila and eastern Chihuahua seems likely, but is not yet established.

The limits of the variation in this subspecies do not correspond closely to those set by Munz (1929) for *Oenothera hartwegii* var. *typica*. The strigose pubescence of Hartweg's type actually excludes it from Munz's description, and the bulk of the present taxon would also not be included. *Oenothera greggii* var. *pringlei* was named to accommodate the strigose-canescens forms, but since Hartweg's original type represents that group of populations var. *pringlei* must be reduced to synonymy. On the basis of leaf width, I have placed some elements of Munz's var. *typica* in *C. hartwegii* subsp. *maccartii*. In addition, a portion of Munz's var. *typica* which included glandular-pubescent individuals is joined with *C. hartwegii* subsp. *filifolius*, as is part of Shinner's *C. hartwegii* var. *hartwegii*. Lastly, some collections with glabrous leaves and stems placed in var. *typica* by Munz and in var. *hartwegii* by Shinner clearly belong with *C. hartwegii* subsp. *fendleri* as it is here constituted. In all previous treatments, the composition of var. *hartwegii* has been extremely heterogeneous. Clear identification of the nature of Hartweg's type and the recognition of larger geographical assemblages have rendered the variation pattern for *C. hartwegii* less confusing, especially with regard to subsp. *hartwegii*. Finally, a few plants assigned to *Oenothera lavandulaefolia* by Munz clearly belong with *C. hartwegii* subsp. *hartwegii* on the basis of their long sepal tips, narrow leaves, and southern distribution.

Considerable variation in leaf width, stature, and degree of pubescence exists in this subspecies. Especially pubescent plants with small leaves occur in Chihuahua and northern Durango. High montane plants tend to be shorter and more tufted, while the stems of low altitude plants are longer and more erect. Broader leaves occur in the latter populations, especially where they intergrade with *C. hartwegii* subsp. *maccartii* in northeastern Mexico and in western Texas, an extensive zone occupied by intermediates between subspp. *hartwegii* and *pubescens*.

In one field study, D. E. Breedlove (personal communication) found anthesis in a population of this form to occur by 1 to 1¾ hours after sunset (San Luis Potosí, *Breedlove 15473*). However, no insects visited the flowers during the period of his observations. In the state of Chihuahua, Mexico I observed several bees (*Agapostemon*, *Apis*) and small butterflies on freshly opened flowers in the midafternoon (*Towner 247*). Anthesis in Chihuahuan populations occurred from 4½ to 2 hours before sunset. Greenhouse-cultivated plants from a wide range of Mexican localities showed great variation in opening times, extending from 4½ hours before sunset to sunset. This variation in anthesis times may be a result of latitudinal or seasonal differences in photoperiod or a product of adapta-

tion to locally differing insect faunas. Regional ecological differentiation may well have occurred within this subspecies since the southern forms from pine forests seem to open much later than those inhabiting scrub and grasslands in the plains and hills of Chihuahua. Hawkmoths are undoubtedly regular evening visitors to all populations of subsp. *hartwegii*. Ultraviolet-absorbing areas on the petals can be nearly absent, present along the basal portion of the veins, or present as a small basal spot (Fig. 8). This suggests that some populations, i.e., those with spots absent, may be exclusively moth-pollinated while those with spots and early anthesis may be visited by bees active in the late afternoon.

Chromosomal variation in this subspecies includes polyploidy, translocation heterozygosity, and extra chromosomes. Two of 11 populations, 1 from Aguascalientes and 1 from Zacatecas, yielded tetraploid counts. Translocation heterozygosity was found in 7 of 17 diploid plants examined and in 6 of 9 populations from which meiotic determinations were obtained. The mean frequency of translocations per plant, 0.4, was the lowest for any taxon in the genus. Four plants of this subspecies had 1 to 4 extra diminutive chromosomes. Examination of hybrids indicated that one population of *C. hartwegii* subsp. *hartwegii* differed from the other taxa in sect. *Salpingia* by one or two translocations.

Introgression of *C. hartwegii* subsp. *hartwegii* with other taxa appears to occur widely, especially with subspp. *pubescens* and *maccartii*. Intermediates between subspp. *pubescens* and *hartwegii* exist in southern West Texas, southeastern Arizona, and probably in northern Chihuahua and Coahuila. Regions of intermediate altitude in northeastern Mexico and along the upper Rio Grande River in southern Texas contain populations varying on a continuum between subspp. *maccartii* and *hartwegii*. As mentioned on p. 99, *C. tubicula* subsp. *strigosus* may represent a stabilized derivative of introgression between *C. tubicula* subsp. *tubicula* and *C. hartwegii* subsp. *hartwegii*. Lastly, plants with narrow leaves, but lacking dense strigose pubescence, occur near Saltillo in southern Nuevo León and may represent introgressants with *C. hartwegii* subsp. *filifolius*, which occurs to the south of that area, or alternatively they may be independent narrow-leaved derivatives of the species.

No examples of sympatry without hybridization have been documented for *C. hartwegii* subsp. *hartwegii* and other taxa. The recent discovery of *C. lavandulifolius* in southern Nuevo León opens the possibility that it might come into contact with *C. hartwegii* subsp. *hartwegii*. Those two taxa proved somewhat intersterile in laboratory crosses, and might not be expected to hybridize extensively in the field.

1b. ***Calylophus hartwegii*** (Benth.) Raven subsp. ***maccartii*** (Shinners) Towner & Raven, *Madroño* 20: 243. 1970.

Calylophus hartwegii (Benth.) Raven var. *maccartii* Shinners, *Sida* 1: 343. 1964.

Oenothera greggii A. Gray var. *pringlei* Munz sensu Munz, *Amer. J. Bot.* 16: 711. 1929, pro parte. *O. pringlei* (Munz) Munz sensu Munz, *N. Amer. Fl.*, ser. 2, 5: 138. 1965, pro parte.

Stems several to many, sparingly branched above, nearly prostrate to ascending, 0.5–5 dm high; plants glandular-pubescent or minutely strigulose. Leaves

sparse to dense on stems, spreading to more or less ascending, narrowly lanceolate to lanceolate or oblanceolate, rarely linear, 6–35 mm long, 1–6 mm wide, nearly glabrous to sparsely strigulose or glandular-pubescent, the tip acute, the base acute-attenuate, the margin subentire to serrulate, usually undulate or undulate-crinkled; axillary leaves present, to 15 mm long. Inflorescence sparsely to densely strigulose. Floral tube 17–45 mm long, 5–12 mm wide at the throat. Sepals 11–27 mm long, 2.5–7 mm wide, with free tips 1–6 mm long, occasionally with purple marginal stripes. Petals nearly orbicular to squarish, 10–30 mm long, frequently fading purple or pinkish, with a conspicuous, large basal ultraviolet-absorptive spot. Filaments 6–12 mm long; anthers 5–9 mm long. Style 25–60 mm long, glabrous above to minutely pubescent basally; stigma 2–4 mm broad; ovary 5–15 mm long, 1.5–2 mm wide. Capsule 10–22 mm long, 2–3 mm wide; seeds 1–2 mm long. Self-incompatible. Gametic chromosome numbers, $n = 7, 14$.

TYPE: UNITED STATES. TEXAS: Starr Co., U.S. Highway 83, 6 mi NW of Rio Grande, in mesquite savannah, 24 March 1963, *Rosa Ena Benavides* 91 (SMU, holotype; TEX, isotype).

Distribution (Fig. 15): Common semiarid grassy flats, in sandy to gravelly soil, often of limestone, frequently with *Prosopis glandulosa*, *Opuntia*, *Acacia*, *Larrea divaricata*, and *Yucca*, on the South Texas Plains and along the Rio Grande from Val Verde, Kinney, Uvalde, and Milam cos., Texas, south to southeastern Coahuila, central Nuevo León and northwestern Tamaulipas. From elevations of ca. 30 m (4 mi NW of Mathis, San Patricio Co., Texas) to ca. 1,500 m (Saltillo, Coahuila). Flowers March to September.

Representative specimens examined:

UNITED STATES. TEXAS: Dimmit Co.: E of Carrizo Springs, *Jones* 28153 (MO, POM). 8 mi S of Catarina, *McGregor* 16774 (DS, KANU). Duval Co.: 10 mi SW of Benavides, *García* 113 (OKLA, SMU, TEX). 16 mi NE of Freer, *Malacara & Gutiérrez* 30 (LL, SMU). San Diego, *Tharp* 6031 (TEX, US). 7 mi E of Freer, *Rodríguez* 104 (OKLA, SMU, TEX). Goliad Co.: Goliad, *Williams* 110 (PH, TEX). Jim Hogg Co.: 2 mi N of Santa Elena, *Ríos & Cavazos* 68 (LL). Jim Wells Co.: 23 mi N of Alice, *Painter et al.* 14436 (LL, TEX). 8 mi N of Alice, *Bruni et al.* 13 (LL). 15 mi NW of Alice, *Castillo* 20 (DS, SMU). Kinney Co.: Spofford, *Treleau in* 1900 (MO). Ca. 20 mi NE of Brackettville, *Strother* 299 (SMU, TEX). 26.0 mi SE of Del Rio, *Towner* 34 (DS). La Salle Co.: Encinal, *Vásquez* 43 (DS). Live Oak Co.: 11.5 mi S of George West, *Cory* 28531 (POM). 8 mi S George West, *Flyr* 353 (DS, SMU). Maverick Co.: 30 mi SW of Eagle Pass, *Bruni* 8 (LL, OKLA, SMU, TEX). 5 mi N of Eagle Pass, *Rowell* 8824 (LL, OKL, OKLA). Eagle Pass, *Schott in* 1852 (F). San Patricio Co.: 4 mi NW of Mathis, *Raven & Gregory* 19386 (DS). Uvalde Co.: 5 mi W of Uvalde, *Munz* 15558 (POM). Sabinal, *Jones* 29563 (POM). Val Verde Co.: Near Comstock city limits, *Warnock & Turner* 696 (SMU). N of Del Rio, *Jones* 28158 (MO, POM). Devil's River, *Earle & Earle* 441 (MO, NY, US). Ca. 20 mi NNW of Del Rio, *McVaugh* 8259 (DS, F, SMU, TEX). Ca. 23.5 mi NW of Del Rio, *Towner* 32 (DS). 3.4 mi SE of Del Rio, *Towner* 33 (DS). Webb Co.: Minera, *Reverchon* 3558 (MO, US). 10 mi S of Laredo, *Cisneros* 15 (LL, OKLA). Laredo, *Crockett* 6444 (LL, US). 11 mi S of Laredo, *Robles* 14 (SMU). 8 mi NW of Laredo, *Ramírez* 45 (DS, SMU). 23 mi NW of Laredo, *McCart* 7270 (OKLA). 9.5 mi S of Laredo, *Cory* 28118 (POM). Zapata Co.: Zapata, *Pérez* 42 (DS). Near Zapata, *Wood* 42 (TEX). 5 mi S of San Ignacio, *Rodríguez* 27 (SMU). 3 mi S of Zapata, *Sánchez* 85 (OKLA, TEX). Zapata, *Guajardo* 32 (LL, SMU). 2 mi SE of Zapata, *González-Arroyo* 92 (LL, OKLA, SMU).

MEXICO. TAMAULIPAS: Along the river road, 20 mi E of the International Highway, *Escalante* 55 (SMU, TEX, OKLA). 3 mi SW of Headquarters, Loreto Ranch, *Crutchfield & Johnston* 5568A (TEX). 50 mi SE of Nuevo Laredo, *García & García* 35 (DS, WTU). NUEVO LEÓN: 24 mi W of Monterrey, *Waterfall & Wallis* 13214, 13215 (RSA, SMU). Monterrey,

Fisher 272 (MO, US). Río Santa Catarina, Monterrey, *Arsène 6306* (MO, US). 65 mi S of Nuevo Laredo, *Frye & Frye 2369* (DS, MO, NY, RM, RSA, SMU, UC, WTU). 9 mi S of Nuevo Laredo, *Frye & Frye 2390* (NY, RSA, UC, US, WTU). 12 mi N of Sabinas Hidalgo, *Barkley & Heard 14535* (F, MO, US). 17 mi NE of Sabinas Hidalgo, *Rodríguez 70* (SMU, TEX). 16 km W of Sabinas Hidalgo, *Domínguez & McCart 8255* (SMU, TEX). 45 mi S of Nuevo Laredo, *McCart et al. 8133* (OKLA, SMU, TEX). Sabinal (?), *Jones 29563* (MO, UC). Monterrey, *Dodge 158* (US). Between Monterrey and Reynosa, along side road to San Juan, *Langman 2870* (DS, PH). Monterrey, *Edwards & Eaton in 1846* (NY). 50 mi S of Laredo, *Hess & Hall 637* (OKL). Ca. 54 mi S of the U.S. border in Laredo, *Towner 35* (DS). 39 mi N of center of Monterrey, *Towner 36* (DS). COAHUILA: 9 km S of Parras, Sierra Negra, *Stanford et al. 158* (ARIZ, MO). Near Díaz (now Piedras Negras), *Pringle 8304* (DS, F, MO, PH, POM, RM, RSA, UC, US). Ciudad de Porfirio Díaz, *Canby 109* (US). Guadalupe, *Aguirre 703* (RSA). Parras, *Aguirre & Reko 82* (NY). Ca. 48 mi N of Saltillo, *Jackson 6722* (KANU). 25 km S of Piedras Negras, *Rinehart 218* (OKL, OKLA, RSA). 13.4 mi S of central Saltillo, *Towner 52, 53* (DS).

Closely related to *Calylophus hartwegii* subsp. *hartwegii*, this subspecies occurs at higher latitudes and lower elevations. It is relatively common in disturbed areas in the grasslands of southern Texas. It corresponds closely to var. *maccartii* as treated by Shinnars except that narrower-leaved plants are included here. The broad leaves, which are frequently oblanceolate, early afternoon anthesis, and sparser, often glandular pubescence serve to distinguish this subspecies from subsp. *hartwegii*. Only leaf dimensions serve adequately in separating subsp. *maccartii* and *filifolius*. Considerable phenotypic variation occurs in subsp. *maccartii* in terms of pubescence, leaf shape, stature, and nature of the leaf margin. Leaf margins may be serrulate, undulate, or subentire.

Pollination was studied near Saltillo, Coahuila, Mexico (*Towner 52, 53*) at a roadside population of *C. hartwegii* subsp. *maccartii*. Anthesis was not observed, but had been completed by 2¼ hours before sunset. Most visitors to the flowers were halictid bees, especially *Evylaeus* and *Agapostemon*, some of them possibly oligoleges. These may have played some part in pollination in the late afternoon and morning in spite of their small size. No large native bees, except for a single *Bombus*, and no hawkmoths were observed visiting flowers, but their involvement cannot be discounted on the limited evidence available.

Greenhouse studies showed anthesis times occurring 3–5 hours before sunset and flowers with large central ultraviolet-absorbing areas. Self-incompatibility was found in the 3 plants available for testing. This suggests that *C. hartwegii* subsp. *maccartii* has perhaps secondarily shifted from hawkmoth pollination, as indicated by its morphology, to bee pollination, as might be inferred from its ultraviolet pattern and behavior.

Two of 10 populations showed tetraploidy, in addition to 1 population intermediate between *Calylophus hartwegii* subsp. *filifolius* and *maccartii*. One plant from each of 2 populations had a single extra diminutive chromosome. Half of 16 plants, representing 5 of 8 diploid populations, were heterozygous for translocations. The mean frequency of translocation heterozygosities was 0.6 per plant, and only one plant had as many as 2. Experimental hybrids between *C. hartwegii* subsp. *maccartii* and other members of sect. *Salpingia* were heterozygous for 1 or 2 reciprocal translocations.

Introgression occurs, as mentioned above, with *C. hartwegii* subsp. *hartwegii* in southern Texas and northeastern Mexico. It also appears to have taken place

with subsp. *pubescens* along the upper Rio Grande in southern Texas, although there is difficulty in recognizing the sources of variation in this region. Two further collections [36 mi W of Monterrey, Coahuila, Mexico, *Towner* 39 (DS). 5 mi W of Marathon, Brewster Co., Texas, *Warnock* 60004 (TEX)] appear to be intermediate between subsp. *maccartii* and *filifolius*, although this may not necessarily have resulted from introgression. The only other taxon of *Calylophus* occurring near *C. hartwegii* subsp. *maccartii* is *C. berlandieri* subsp. *berlandieri*. The two are essentially intersterile, but in the South Texas Plains have often been mistaken for one another because there they tend to resemble each other in leaf shape and character of the margin.

1c. ***Calylophus hartwegii*** (Benth.) Raven subsp. ***filifolius*** (Eastw.) Towner & Raven, *Madroño* 20: 243. 1970.

Oenothera tubicula A. Gray var. *filifolia* Eastw., Proc. Calif. Acad. Sci., ser. 3, 1: 72. 1897. *Galpinsia filifolia* (Eastw.) Heller, Cat. N. Amer. Pl., ed. 2. 8. 1900. *Oenothera hartwegii* Benth. var. *filifolia* (Eastw.) Munz, Amer. J. Bot. 16: 707. 1929. *Calylophus hartwegii* (Benth.) Raven var. *filifolius* (Eastw.) Shinnars, Sida 1: 345. 1965. *Oenothera hartwegii* var. *fendleri* (A. Gray) A. Gray subvar. *filifolia* (Eastw.) H. Lév., Monogr. Onoth. 335. 1908.

Oenothera hartwegii Benth. var. *typica* sensu Munz, Amer. J. Bot. 16: 706. 1929, pro parte. *Calylophus hartwegii* (Benth.) Raven var. *hartwegii* sensu Shinnars, Sida 1: 342. 1964, pro parte. *Oenothera hartwegii* var. *hartwegii* sensu Munz, N. Amer. Fl., ser. 2, 5: 139. 1965, pro parte.

Stems several to many, moderately to densely branched above, decumbent and spreading to somewhat ascending, 0.5–4 dm high; plant minutely glandular-pubescent throughout, more densely so on the ovary and inflorescence, infrequently sparsely strigulose on the ovary and leaves. Leaves moderately well-spaced to dense on the stem, spreading to ascending, filiform to narrowly lanceolate, 3–45 mm long, 0.4–3(–4) mm wide, the tip acute, the base acute-attenuate, the margin entire to remotely serrulate, occasionally undulate; axillary leaves present, to 10(+) mm long. Floral tube 16–50 mm long, 4–14 mm wide at the throat, occasionally fading pinkish. Sepals 7–17 mm long, 3–7 mm wide, with free tips 0.5–4 mm long, frequently with purple spotting and occasionally with a purple marginal stripe. Petals suborbicular to somewhat rhomboidal, 12–23 mm long, occasionally fading pinkish, with a basal ultraviolet-absorptive spot of moderate to large size. Filaments 6–13 mm long; anthers 6–11 mm long. Style 26–60 mm long, glabrous above, glabrous or minutely pubescent basally; stigma 1.5–4 mm broad; ovary 4–13 mm long, 1–2 mm wide. Capsule 7–22 mm long, 2–3 mm wide; seeds 1.2–2 mm long. Self-incompatible. Gametic chromosome number, $n = 7$.

TYPE: UNITED STATES. NEW MEXICO: White Sands, probably in Otero Co., August 1896, *T. D. A. Cockerell* (CAS).

Distribution (Fig. 16): Highly local, but often abundant, almost always on semiarid gypsum flats, dunes, or outcrops, frequently with *Larrea divaricata*, *Yucca*, or *Juniperus*, from Otero and Torrance cos., New Mexico south and east through the Trans-Pecos and southern Panhandle regions of Texas, thence northeast to Cottle Co., Texas and southward from widely scattered localities in cen-

tral Chihuahua and Coahuila. Occurring from elevations of ca. 600 m (7 mi N of Spur, Dickens Co., Texas) to ca. 1,850 m (7.2 mi SE of Willard, Torrance Co., New Mexico). Flowers May to October.

Representative specimens examined:

UNITED STATES. NEW MEXICO: Chaves Co.: 20 mi S of Roswell, *Earle & Earle* 293 (MO, NY, POM, RM, UC, US). 2 mi E of Bottomless Lakes State Park Headquarters, *Hess* 73 (WTU). 56.7 mi SE of Vaughn, *Towner* 125 (DS). 18.7 mi N of Roswell on U.S. 285, *Towner* 128 (DS). De Baca Co.: 22 mi S of Fort Sumner, *Brooks & Stephens* 25763 (DS). Dona Ana Co.: Jornada Game Reserve, *Wooton*, no date (US). Eddy Co.: 3 mi NW of Texas state line on U.S. 62/180, *Raven & Gregory* 19156 (DS). 6 mi SW of White's City, *Munz & Gregory* 23357 (POM, UC, WTU). 11.4 mi SW of White's City, *Towner* 22 (DS). Lea Co.: 55–60 mi E of Roswell, *Palmer* 62 (F). Lincoln Co.: White Mts., 5,400 ft, *Wooton* 181 (ARIZ, DS, GH, MO, NY, POM, RM, UNM, UC, US). 22 mi N of Carrizozo, *Brooks & Stephens* 25957 (DS). Otero Co.: Round Mt., along Tularosa Creek in Sacramento Mts., *Wooton in 1899* (ARIZ, DS, NMC, NY, POM, RM, US). White Sands National Monument, *Munz & Gregory* 23335 (POM). White Sands National Monument, 2 mi W of headquarters, *Towner* 11 (progeny, DS). Torrance Co.: Near Willard, *Wooton* 2730 (COLO, DS, RM, US). 7.2 mi SE of Willard, *Towner* 122 (DS). TEXAS: Culberson Co.: 2 mi SE of U.S. 62/180 at New Mexico line, *McVaugh* 8164 (DS, GH, LL, SMU, TEX). 30 mi N of Van Horn, *Waterfall* 4122 (GH). Dickens Co.: 7 mi N of Spur, *Moss* 19 (OKLA). Ector Co.: 1 mi E of jct. of Texas 185 and U.S. 385, *Gregory* 424 (DAO, DS, RSA, UC). Gaines Co.: 15 mi E of Seminole, *Lundell & Lundell* 16955 (LL). Howard Co.: Big Springs, *Tracy* 8306 (F, GH, MO, NEB, NY, TEX, US). Hudspeth Co.: Gypsum quarry E of Finley, *Waterfall* 5023 (GH, MO). Kent Co.: 2 mi W of Clairemont on U.S. 380, *Correll & Johnston* 22107 (LL). Loving Co.: Along Salt Creek near highway 285, N of Orla, *Correll & Correll* 26016 (Mixed with *C. hartwegii* subsp. *pubescens*, LL). Martin Co.: E of Stanton, *Lundell & Lundell* 16916 (LL). Midland Co.: 4 mi E of Midland, *Cory* 42030 (POM, TEX). Nolan Co.: Sweetwater, *Reverchon* 1285 (F, MO). Ward Co.: 9.5 mi S of Monahans, *Gregory* 174 (RSA, UC, WTU). Winkler Co.: 1 mi N of southern county line on highway 18, *Irving* 69 (SMU, TEX).

MEXICO. COAHUILA: Morillo, Saltillo, *Lyonnet* 3497 (US). Saltillo, *Fisher in 1926* (DS). 6 mi N of La Ventura, *Johnston* 7644 & *Shreve* 8726 (ARIZ, UC, US). NUEVO LEÓN OR COAHUILA: Vanegas-Saltillo road, alkali plain, *Lundell* 5721 (ARIZ, F, POM). CHIHUAHUA: 13 mi S of Gallegos, *Breedlove* 15734 (DS). ZACATECAS: Intersection of highways 49 and 45, *Cruden* 1238 (TEX). No locality: Mexico, *Gregg* 33 (MO).

Calylophus hartwegii subsp. *filifolius*, which is largely endemic to gypsum soils, may include some convergent populations of independent origin. The Texas and Coahuila populations are widely separated, with no collections having yet been obtained in the intervening region, a span of over 650 km.

I have retained here certain populations with broader leaf dimensions than were included by Shinnery or Munz. Plants from the type locality do not all have filiform leaves, although collections from the White Sands area do include the narrowest-leaved plants in the species. Inclusion of the broader-leaved populations here simplifies the variation pattern in *C. hartwegii* subsp. *hartwegii* and renders subsp. *filifolius* a major geographical race which is nonetheless phenetically discrete. In West Texas and southeastern New Mexico this taxon is abundant on plains at about 600–1,200 m elevation. Some variability is shown by this subspecies in terms of leaf width, petal shape, the presence and distribution of anthocyanins, and length of the free sepal tips. Pubescence is relatively uniform, with nearly all plants being glandular-pubescent, and only a few being even minutely strigulose.

The pollination studies of Gregory (1964; as *Oenothera hartwegii*) in Ector and Ward cos., Texas indicated that flowers of *C. hartwegii* subsp. *filifolius* were



FIGURE 16. Distributions of *Calylophus hartwegii* subsp. *pubescens* (dots), *C. hartwegii* subsp. *fendleri* (open circles), and *C. hartwegii* subsp. *filifolius* (triangles).

open well before sunset and were visited by hawkmoths in the evening and sometimes by bees in the afternoon. Greenhouse studies showed anthesis to occur 3–6 hours before sunset. Ultraviolet-absorbing spots at the base of each petal were fairly large, presenting conspicuous regions of high contrast which would be visible to diurnal insects. Tests for self-incompatibility on 6 plants all proved positive.

Cytogenetically, *C. hartwegii* subsp. *filifolius* exhibits a great deal of variation, with plants averaging 1.7 translocation heterozygosities. Ten of 12 plants from 8 populations were heterozygous. The maximum association of chromosomes observed consisted of a ring of 12 and a bivalent, present in a plant grown from seed collected in Winkler Co., Texas (*Irving 69*). As many as 11 extra diminutive chromosomes were observed in plants from that population, with some being possessed by each of the 4 plants examined. No other population demonstrated extra chromosomes, and no tetraploid or higher counts were obtained from this subspecies. One possible intermediate between *C. hartwegii* subsp. *maccartii* and *filifolius*, as mentioned before, was tetraploid (*Towner 39*). Crosses of *C. hartwegii* subsp. *filifolius* with other forms in sect. *Salpingia* demonstrated complete homology with *C. tubicula*, *C. hartwegii* subsp. *fendleri*, and *C. hartwegii* subsp. *pubescens*, and one or two translocation differences from the other taxa.

Calylophus hartwegii subsp. *filifolius* intergrades somewhat with *C. hartwegii* subsp. *fendleri* in the southern Texas Panhandle and in New Mexico, but hybridization is limited by the altitudinal separation of these subspecies. Similarly, there is limited hybridization with *C. hartwegii* subsp. *pubescens* in the same regions. Possible hybridization with *C. hartwegii* subsp. *maccartii* and *C. hartwegii* subsp. *hartwegii* was treated under those taxa. Sympatry without hybridization occurs in New Mexico where *C. berlandieri* and *C. serrulatus* occasionally come into contact with this subspecies.

1d. ***Calylophus hartwegii*** (Benth.) Raven subsp. ***fendleri*** (A. Gray) Towner & Raven, *Madroño* 20: 243. 1970.

Oenothera fendleri A. Gray, Mem. Amer. Acad. Arts., n.s., 4: 45. 1849. *O. hartwegii* Benth. var. *fendleri* (A. Gray) A. Gray, Pl. Wright. 2: 58. 1853. *Galpinsia hartwegii* (Benth.) Britton (var.) *fendleri* (A. Gray) Small, Bull. Torrey Bot. Club 23: 186. 1896. *G. fendleri* (A. Gray) Heller, Cat. N. Amer. Pl., ed. 2: 8. 1900.

Oenothera hartwegii Benth. var. *typica* sensu Munz, Amer. J. Bot. 16: 706. 1929, pro parte. *Calylophus hartwegii* (Benth.) Raven var. *hartwegii* sensu Shinnars, Sida 1: 342. 1964, pro parte. *Oenothera hartwegii* var. *hartwegii* sensu Munz, N. Amer. Fl., ser. 2, 5: 139. 1965, pro parte.

Stems one to several, sparingly to moderately branched above, ascending to more or less erect, 1.5–4 dm high; plant glabrous throughout, infrequently minutely and sparingly glandular-pubescent. Leaves sparse to dense on stems, more or less ascending, linear to oblanceolate or lanceolate, 10–50 mm long, 1.5–10 mm wide, the tip acute, the base acute-attenuate to obtuse, infrequently nearly clasping, the margin entire to subentire, infrequently undulate; axillary leaves usually absent, to 10 mm long when present. Floral tube 30–50 mm long,

7–15 mm wide at the throat, sometimes with purple lines, frequently fading purplish or orange. Sepals 9–28 mm long, 4–10 mm wide, with free tips 0.5–3 mm long, occasionally with purple margins or spotting. Petals obovate to somewhat rhomboidal or squarish, 10–30 mm long, usually fading purplish or reddish, with a basal ultraviolet-absorptive spot small or absent. Filaments 5–12 mm long; anthers 5–13 mm long. Style 40–75 mm long, glabrous above, minutely pubescent basally; stigma 2–6 mm broad; ovary 7–20 mm long, 1–2 mm wide. Capsule 10–40 mm long, 2–3 mm wide; seeds 1–1.5 mm long. Self-incompatible. Gametic chromosome number, $n = 7$.

TYPE: UNITED STATES. NEW MEXICO: without specific locality, “probably Santa Fe,” 1847, A. Fendler 230 (GH, lectotype; GH, MO, NY, P, PH, US, isolectotypes); cf. Munz, Amer. J. Bot. 16: 708. 1929. The sheets assigned this number are probably a mixture of collections from the originally published localities, i.e., Santa Fe, on the Río del Norte (Rio Grande), and from Rock Creek eastward to the Cimarron River.

Distribution (Fig. 16); Uncommon on clay or gravelly soils, occasionally calcareous, from high plains with *Prosopis glandulosa* and *Juniperus*, to montane forests with *Juniperus*, *Pinus edulis*, and occasionally *Pinus ponderosa*, from Barber and Morton cos., Kansas, south through western Oklahoma and widely scattered sites in the Texas Panhandle to eastern Chihuahua, central Trans-Pecos Texas, central and western New Mexico, and east-central Arizona. Elevational distribution from ca. 370 m (Agawam, Grady Co., Oklahoma) to 2,200 m (17 mi N of Alpine, Apache Co., Arizona). Flowers April to October.

Representative specimens examined:

UNITED STATES. KANSAS: Barber Co.: NW corner of county, *Baker in 1904* (NY). Gypsum hills, *Hitchcock 689* (GH, NMC, NY, RM, US). 6 mi W of Medicine Lodge, *Stephens 11150* (KANU, OKLA). 7 mi W of Medicine Lodge, *McGregor 14243* (KANU, SMU, US). 7 mi SW of Medicine Lodge, *McGregor 14472* (SMU, US). Sandy soil S of Coats, *Bondy in 1936* (ARIZ, CAN, F, MO, OKL, OKLA, RM). 7 mi S of Sun City, *McGregor 14019* (KANU). Morton Co.: 4 mi W of Rolla, *McGregor 12858* (KANU, SMU, US). OKLAHOMA: Blaine Co.: 5 mi NE of Watonga, *Stephens & Brooks 20819* (KANU). Roman Nose State Park, *Goodman & Waterfall 4185* (GH, OKL, OKLA). Grady Co.: 8 mi SW of Chickasha, *Pearce 767* (SMU). Greer Co.: 7.7 mi S of Mangum, *Towner 79* (DS). 2.6 mi S of Mangum, *Towner 85* (DS). 0.5 mi S and 4.3 mi W of Brinkman, *Towner 86* (DS). Harmon Co.: 10 mi S of McQueen, *Stephens & Brooks 20758* (DS, KANU). Harper Co.: Near Buffalo, *Stevens 535* (DS, GH, MO, NY, OKL, OKLA, US). 17 mi E and 7 S of Buffalo, *Stephens & Brooks 21685* (DS, KANU). Kiowa Co.: Snyder, *Stevens 1198* (OKLA). Roger Mills Co.: 18 mi N of Cheyenne, *Waterfall 11897* (OKLA, SMU, TEX, US). Ca. 8 mi E of Strong City, *Towner 156* (DS). Woods Co.: 37 mi W of Alva, *Stratton 6384* (KANU, OKL). Woodward Co.: 24 mi N of Mooreland, *Brooks & Stephens 21658* (DS, KANU). TEXAS: Hemphill Co.: Prairies N of Canadian, *Eggert in 1901* (MO). Jeff Davis Co.: 14.8 mi N of Marfa city limits, *Parnell 68-T-30* (DS). 8 mi S of Fort Davis, *Munz & Gregory 23384* (RSA, UC). 3.8 mi W of Fort Davis, *Gregory 134* (NY, RSA, WTU). Mesa S of Fort Davis, *Andrews 63* (COLO, GH). Limpia Canyon, Davis Mts., *Bray in 1902* (TEX). Presidio Co.: 8 mi E of Marfa, *Warnock 7916* (LL, SMU, TEX). 8 mi NW of Marfa, *Jackson in 1964* (progeny only, DS). 13.0 mi NW of Marfa, *Towner 25* (DS). 11.9 mi NW of Marfa, *Towner 26* (DS). 10.4 mi NW of Marfa, *Towner 27* (DS). Randall Co.: Bottom of canyon, Palo Duro Canyon State Park, *Lundell & Lundell 11442* (LL, SMU). Wilbarger Co.: 1.5 mi S of Harrold, *Whitehouse 9764* (ARIZ, SMU, UC, US). NEW MEXICO: Catron Co.: Mangas Creek, *Rusby in 1880* (US). Mangas Canyon, *Greene in 1880* (F, MO, NY, PH). Grant Co.: Vicinity of Gila, *Maguire 11630* (DAO, NY, WTU). Lincoln Co. (?): Gallinas Mts., *Wooton 2741* (US). Otero Co.: 8 mi E of Mescalero, *Parker 2556a* (ARIZ, COLO). Above Mescalero, White Mts., *Wooton in*

1895 (US). Rio Arriba Co.: Arroyo de Agua, *Gregory* 588 (UC). Sandoval Co.: San Isidro, *Benedict* 2311 (US). San Miguel Co.: Near Pecos, *Standley* 4952 (GH, MO, NMC, NY). Santa Fe Co.: 19 mi W of Santa Fe, along the Rio Grande R., *Heller & Heller* 3622 (MO, NY, US). Socorro Co.: 0.4 mi S of Magdalena, *Towner* 119 (DS). Torrance Co.: 3.1 mi NW of Cedarvale, *Towner* 123 (DS). 2.6 mi W of Willard, *Towner* 121. Valencia Co.: 8 mi E of Ramah, *Wootton in 1906* (NMC, NY, US). ARIZONA: Apache Co.: 17 mi N of Alpine, *Breedlove* 14298 (DS). 7.9 mi N of Alpine, *Towner* 110 (DS). 4.5 mi N of Nutrioso, *Towner* 111 (DS). 8.0 mi N of Nutrioso, *Towner* 112 (DS). Coconino Co.: Walnut Canyon, *MacDougal in 1898* (ARIZ, F, GH, NY, PH, RM, UC, US). Flagstaff Cemetery, *Demaree* 42847 (ARIZ, DS, OKLA, RSA, SMU). Navajo Co.: Near Heber, *Parker et al.* 6832 (ARIZ, F). 12 mi N of Whiteriver, *Goodman & Hitchcock* 1298 (DS, F, MO, NY, PH, UC).

MEXICO. CHIHUAHUA: 11 mi E of Highway 16 on road to new lake on Río Conchos, *Powell et al.* 2032 (TEX).

A race with distinctive characters of distribution, morphology, and floral behavior, *Calylophus hartwegii* subsp. *fendleri* definitely merits recognition, contrary to the opinion of Shimmers (1964). Late anthesis, glabrous vegetative parts, and distribution at relatively high altitudes or latitudes are strongly correlated in this form. In the northern part of its range, it occurs at intermediate or low altitudes, but in Arizona and New Mexico it ranges up into the coniferous forests. Leaf dimensions not being of critical importance for delimiting this subspecies has allowed the inclusion of elements from Munz's *Oenothera hartwegii* var. *hartwegii*. Thus considerable variation in leaf dimension is retained in *C. hartwegii* subsp. *fendleri*, which attains a large and broad leaf size for the species, especially in collections from the Great Plains. Relatively narrow-leaved forms from the mountains of Trans-Pecos Texas belong here, although they have been traditionally placed with *Oenothera hartwegii* var. *hartwegii*.

The type series of *Evylaeus galpinsiae* (Cockerell) was collected from *Calylophus hartwegii* subsp. *fendleri* near Pecos, New Mexico where the bees were active at 7:30 in the evening (Cockerell, 1903). Pollination studies of Gregory (1964) in Jeff Davis Co., Texas (as *Oenothera hartwegii*) suggested that anthesis occurs near sunset and that pollination is largely accomplished by hawkmoths. My field observations in Grant Co., New Mexico (*Towner* 244) differed somewhat from Gregory's in that numerous bees of the genera *Sphex* and *Evylaeus* were active gathering pollen from this subspecies for about one hour starting at sunset. As observed by Gregory, hawkmoths visited the flowers heavily in the early evening. Infrequent visits by bees were seen in the morning. Field observations at this site and elsewhere in New Mexico indicated that anthesis occurs at about sunset, and flowers on cultivated plants opened within an hour before or after sunset. Photography under ultraviolet light showed plants to have either no spots of absorption on the petals or only very small ones (Fig. 10). Two plants were checked and found to be self-incompatible.

No tetraploid individuals have been found in this subspecies. Sixteen of 23 plants from 12 of 15 populations were heterozygous for translocations, with a mean number of 0.9 heterozygosities per plant. The maximum number of heterozygosities exhibited was 2, seen in 5 plants. Hybrids with other taxa in sect. *Salpingia* behaved identically to those involving *C. hartwegii* subsp. *filiifolius* in terms of chromosome pairing. Four to 5 extra diminutive chromosomes were observed in 3 plants, each from a different population.

Instances of hybridization with *C. hartwegii* subsp. *pubescens*, particularly in

Oklahoma, seem relatively common, and the two subspecies are not separated by large ecological differences. One population in Harmon Co., Oklahoma consisted of both subspecies and intermediates. Cases of intergradation with other taxa have been discussed in previous sections. *Calylophus hartwegii* subsp. *fendleri* occurs frequently with *C. serrulatus* in Oklahoma, with no indication of hybridization. A population in Torrance Co., New Mexico was found growing with *C. lavandulifolius*, and again no intermediates or putative hybrids were observed.

1e. ***Calylophus hartwegii* (Benth.) Raven subsp. *pubescens* (A. Gray) Towner & Raven, Madroño 20: 243. 1970.**

Oenothera greggii A. Gray var. *pubescens* A. Gray, Pl. Wright. 1: 72. 1852. *Calylophus hartwegii* (Benth.) Raven var. *pubescens* (A. Gray) Shinnars, Sida 1: 344. 1964.

Oenothera greggii A. Gray, Mem. Amer. Acad. Arts, n.s., 4: 46. 1849. *Galpinsia greggii* (A. Gray) Small, Bull. Torrey Bot. Club 23: 186. 1896. *Oenothera hartwegii* Benth. var. *fendleri* (A. Gray) A. Gray subvar. *filifolia* H. Lév. f. *thymifolia* H. Lév., Monogr. Onoth. 335. 1908, based on MO isotype. *O. greggii* var. *typica* Munz, Amer. J. Bot. 16: 709. 1929. TYPE: Mexico, Durango, hill SE of Pelayo, ca. 60 mi NW of Torreón, 8 May 1847, Josiah Gregg 591 (GH, holotype; MO, NY, isotypes).

Oenothera lampasana Buckley, Proc. Acad. Nat. Sci. Philadelphia 1861: 454. 1961. *Galpinsia lampasana* (Buckley) Wooton & Standley, Contr. U.S. Natl. Herb. 16: 152. 1913. *Oenothera greggii* A. Gray var. *lampasana* (Buckley) Munz, Amer. J. Bot. 16: 710. 1929. TYPE: United States, Texas, Lampasas Co., prairies, 1860–1861, S. B. Buckley (PH).

Galpinsia interior Small, Fl. S.E. U.S. 845, 1335. 1903. TYPE: United States, Nebraska, Cherry Co., Fort Niobrara, 25 June 1888, T. E. Wilcox (NY). This locality is more than 300 mi N of the known range of this subspecies and probably resulted from dispersal by accident or human intent, or the label may have been switched.

Galpinsia camporum Wooton & Standley, Contr. U.S. Natl. Herb. 16: 152. 1913. *Oenothera camporum* (Wooton & Standley) Tidestrom in Tidestrom & Kittell, Fl. Ariz. & N. Mex. 278. 1941. TYPE: United States, New Mexico, Lea Co., Knowles, 29 July 1890, E. O. Wooton (US-564592, holotype; NMC, POM, US, isotypes).

Stems several, moderately branched above, decumbent to more or less erect, 1–5 dm high; plant usually covered throughout with long spreading trichomes, most densely on the ovary, inflorescence, and upper stem, occasionally also with short glandular or nonglandular trichomes. Leaves somewhat sparse to dense on the stem, most commonly spreading to reflexed downward, sometimes more or less ascending, very narrowly elliptic or narrowly lanceolate to ovate, 5–40 mm long, 1.5–12 mm wide, the tip acute, the base acute to truncate or subcordate and clasping, the margin entire to sparsely serrulate, occasionally undulate-crinkled; axillary leaves often absent or much reduced, occasionally to 15 mm long. Floral tube 20–50 mm long, 4–20 mm wide at the throat, only rarely with purple stripes, occasionally fading purplish. Petals obovate to somewhat rhomboidal or squarish, 12–35 mm long, frequently fading pinkish or purplish, with a basal ultraviolet-absorptive spot of small or moderate size. Filaments 5–12 mm long; anthers 4–13 mm long. Style 25–70 mm long, glabrous above, minutely pubescent basally; stigma 1.5–5 mm broad; ovary 5–30 mm long, 1–3 mm wide. Capsule 6–35 mm long, 2–3 mm wide; seeds 1–1.7 mm long. Self-incompatible. Gametic chromosome numbers, $n = 7, 14$.

TYPE: UNITED STATES. TEXAS: dry hills beyond the Pecos River, probably from Pecos Co., August 1849, Charles Wright 199 (GH, holotype; GH, NY, PH,

US, isotypes). The locality was calculated from the dates and account of Wright's trip given by McKelvey (1955: 1067-1068).

Distribution (Fig. 16): Common and colonial in moderately dry open places, plains, and hills, in sandy to gravelly soil, often of limestone or gypsum, frequently with *Prosopis glandulosa* and *Juniperus*, from Baca Co. and eastern Las Animas Co., Colorado and Morton and Meade cos., Kansas, to western Oklahoma and the Texas Panhandle, throughout central and Trans-Pecos Texas, thence west through eastern and southern New Mexico to central and southeastern Arizona; also south very locally in central Coahuila and northeastern Durango. Elevational distribution from 200 m (10.5 mi E of Weatherford, Parker Co., Texas) to 2,100 m (2.4 mi NW of Corona, Torrance Co., New Mexico). Flowers March to October.

Representative specimens examined:

UNITED STATES. COLORADO: Baca Co.: 20 mi S of Pritchett, *Harrington* 3325 (RSA). 27 mi S of Pritchett, *Weber* 4608 (COLO, UC, WTU). Las Animas Co.: 7 mi S and 16 E of Kim, *Weber* 4387 (COLO). 4 mi W of Andrix, *Rogers* 4952 (COLO, US). KANSAS: Clark Co.: 10 mi S of Ashland, *Rydberg & Imler* 744 (NY). Meade Co.: 8 mi S and 7 E of Meade, *Horr in 1957* (KANU). SE corner of county, above Wolf Canyon, *Horr* 3612 (KANU). Morton Co.: Stony hills, *Hitchcock* 166 (GH, MO, NMC, NY, POM, RM, US). Point of Rocks, *Hitchcock* 634 (GH). On Cimarron R., N of Elkhart, Point of Rock, *Rydberg & Imler* 942, 943 (MO, NEB, NY). Point of Rocks, 7 mi N and 4 W of Elkhart, *Stephens* 11258 (KANU). No county: SW Kansas, *Plank in 1886* (GH). OKLAHOMA: Beckham Co.: 8 mi N of Sayre, *Wiedman in 1959* (OKL, OKLA). 6 mi S of Elk City, *Eskew* 1503 (GH, KANU, OKL, OKLA). 1.7 mi W and 2.4 N of Elk City, *Stratton* 6835 (KANU, OKLA). Cimarron Co.: 16 mi SE of Kenton, *Waterfall* 7433 (OKL, OKLA, TEX). 2 mi N of Kenton, *Hopkins & van Valkenburgh* 5754 (NY, RM, SMU). Custer Co.: 1 mi W and 0.3 S of Weatherford, *Waterfall* 442 (OKLA, POM). Canyon rims, Clinton, *Demaree* 12466 (ARIZ, GH, MO, NY, OKL, PH, POM, SMU, US). 10 mi W of Clinton, *Munz & Gregory* 23508 (RSA). Ellis Co.: Near Shattuck, *Clifton* 3174 (GH, OKLA). Greer Co.: 2 mi S of Mangum, *Robbins* 3038 (NY, OKL). 3 mi S of Mangum, *Stephens* 20812 (DS). 4.5 mi S of Mangum, *Towner* 82 (DS). Harmon Co.: Near Hollis, *Stevens* 1162 (DS, GH, MO, NY, OKL, OKLA, US). 13.5 mi W of Mangum, *Waterfall* 7174 (OKL, OKLA). Jackson Co.: 3 mi N and 1 W of Eldorado, *Waterfall* 9008 (OKL, OKLA). Kiowa Co.: 3 mi W of Gotebo, *Goodman* 6274 (OKL, RSA, UC). Roger Mills Co.: Red lands, *Engleman* 417, 418 (OKL). 2.5 mi S of Cheyenne, *Wiedeman* 183 (OKL, OKLA). Texas Co.: Goodwell, *Butler* 85 (OKLA). 5.5 mi E of Hardesty, *Stephens & Brooks* 21775 (DS). 7 mi NE of Texhoma, *Waterfall* 9123 (GH, OKL, OKLA). TEXAS: Brewster Co.: Glass Mts., *Tharp* 3629 (US). 4 mi S of Alpine, *Munz & Gregory* 23395 (RSA, UC). Hot Springs area, *Sperry* 1732 (GH). 3.3 mi W of Alpine, *Towner* 28 (DS). Brown Co.: 8.2 mi S of Brownwood, *Towner* 63 (DS). Callahan Co.: Ca. 17 mi SE of Abilene, *Henderson* 64-53 (DS). Coke Co.: 5.2 mi SE of Bronte, *Raven & Gregory* 19279 (DS). Coleman Co.: 14.3 mi N of Coleman, *Towner* 75 (DS). Comanche Co.: 2 mi E of Comanche, *Deckmeier* 17 (LL, SMU, TEX). Concho Co.: 2.5 mi W of Eden, *Munz & Gregory* 23425 (RSA, UC, WTU). 2.8 mi N of Eden, *Raven & Gregory* 19277 (DS). Culberson Co.: 27 mi SW of White's City, New Mexico, *Munz & Gregory* 23364 (RSA, UC). 10 and 12 mi N of Van Horn, *Waterfall* 4095 (ARIZ, GH, MO, NY). Victoria Canyon, Sierra Diablo, *Correll & Rollins* 23783 (LL). 25.6 mi SW of White's City, New Mexico, *Towner* 23 (DS). Glasscock Co.: 3 mi E of Garden City, *Munz & Gregory* 23420 (RSA, UC, WTU). Hardeman Co.: 1 mi N of Quanah, *Stephens* 20721 (DS). Irion Co.: 30 mi N of Barnhart, *Raven & Gregory* 19211 (DS). Lampasas Co.: Lampasas, *Reverchon* 1302 (DS, F, MO, NY, PH, UC, US). Maverick Co.: Eagle Pass, *Havard s.n.* (US). Mills Co.: 0.9 mi N of center of Goldthwaite, *Towner* 70 (DS). Pecos Co.: 25 mi NW of Sanderson, *Munz & Gregory* 23405 (RSA, UC, WTU). Potter Co.: 3.1 mi N of U.S. 66 on Farm Road 1719, *Towner* 93 (DS). 11.3 mi N and 3.9 W of central Amarillo, *Towner* 192 (DS). Presidio Co.: Ca. 35 mi S of Marfa, Bunton Flats, *Warnock* 46621 (RSA). Ca. 3 mi SW of Marfa, *Hinckley* 706 (LL). 12 mi N of Shafter, *Scuddy* 396 (OKLA). Marfa, *Eggleston* 17341 (US). Real Co.: Leakey, *Palmer* 10149 (DS, PH, POM). Roberts Co.: 24 mi

S of Perryton, *Anderson* 2988 (KSC). Taylor Co.: Camp Barkeley, *Tolstead* 7065 (MO, SMU, UC). Terrell Co.: 6.7 mi E of Sanderson, *Raven & Gregory* 19202 (DS). 6.3 mi E of Sanderson, *Gregory* 275 (DAO, RSA, UC). 9.6 mi W of Dryden, *Parks et al.* 305 (LL, SMU). Uvalde Co.: Sabinal, *Palmer* 11514a (MO). By Sabinal R., *McKelvey* 1879 (GH, POM). Uvalde, *Dobie in 1930* (TEX). Val Verde Co.: Pumpville turnoff, *Warnock* 11313 (LL, SMU). Ca. 5 mi W of Langtry, *Warnock & Cameron* 9937 (LL, SMU). Ward Co.: Near Monahans, *Wheeler in 1938* (LL). Wheeler Co.: Ca. 0.5 mi W of Shamrock, *Towner* 88 (DS). Counties unknown: Near Mt. Carmel, Rio Grande, *Parry* 369 (NY, PH). On the Rio Grande, *Wright in 1848* (MO). Between Austin and Stephenville, *Kagan in 1966* (TEX, biochemical voucher). NEW MEXICO: Chaves Co.: Ca. 5 mi N of Roswell, *Towner* 126 (DS). 13.5 mi W of Hope, *Towner* 13 (DS). Ca. 8 mi E of Elk, *Towner* 12 (DS). De Baca Co.: N side of Fort Sumner, *Shinners* 20922 (SMU). Dona Ana Co.: Organ Mts., *Wooton in 1900* (NMC, POM, RM, US). Eddy Co.: Near Three Forks of Rocky Arroyo, Guadalupe Mts., *Wilken* 1734 (PH, US). 1.5 mi ENE of headquarters, Carlsbad Caverns National Park, *Dole* 74 (UC). Junction of Delaware Creek and Pecos R., *Pope in 1835* (GH). Memorial Hospital, N end of Carlsbad, *Munz & Gregory* 23355 (RSA, UC). Lea Co.: 1-11 mi N of Hobbs, *Pearce* 2569 (ARIZ). 60 mi E of Roswell, *Palmer* 66 (F). Lincoln Co.: Ca. 15 mi W of Roswell, *Dunn* 8700 (RSA). 10 mi E of Capitan, *Hitchcock et al.* 4201 (DS, UC, WTU). Hando (Hondo?) Hill, *Wooton in 1904, 1906* (NMC). Otero Co.: 9 mi NE of Alamogordo, *Munz & Gregory* 23337 (RSA, UC, WTU). Quay Co.: Ca. 9 mi W of Tucumcari, *Towner* 94 (DS). 8 mi SW of Tucumcari, *Shinners* 21062 (SMU). 8 mi S of San Juan, *Stephens & Brooks* 25573 (DS). Roosevelt Co.: Portales Springs, *Martin* 784 (WTU). Near Causey, *Wooton in 1909* (NMC). Sierra Co.: Berendo Creek, *Metcalfe* 1574 (F, GH, MO, NMC, NY, POM, UC, US). Torrance Co.: 2.4 mi NW of Corona, *Towner* 124 (DS). Union Co.: Ca. 4 mi N of Moses, *York & Rodgers* 147, 149 (SMU, TEX). ARIZONA: Cochise Co.: 15 mi E of Bernardino, *Benson* 10284 (ARIZ, POM, UC). 6 mi NW of Chiricahua, *Gould & Pultz* 3155 (ARIZ, GH, UC). 6 mi W of entrance to Chiricahua National Monument, *Gregory* 408, 411 (DAO, DS, RSA, UC, WTU). 3 mi E of Dos Cabezas, *Maguire* 11152 (DAO, GH, NY, UC, WTU). Mescal (ca. 7 mi W of Benson), *Thornber* 4312 (ARIZ, OKLA, SMU). Dragoon, *Trogstadt* 1068 (ARIZ, NMC). Ca. 3 mi E of Cochise Stronghold, Dragoon Mts., *Towner* 161 (DS). Gila Co.: 1 mi N of Black R., San Carlos Indian Reservation, *Goodman & Hitchcock* 1287 (DS, F, MO, NY, PH, POM, UC). 1 mi N of Blackriver Road, *Granfelt in 1960* (ARIZ). Between Globe and Cooley (Coolidge?), *Nelson* 10372 (DS, MO, NY, mixture with *C. lavandulifolius*). Pima Co.: Redington, *Goodding in 1935* (ARIZ). Tucson-Redington Road, San Pedro Valley, *Brass* 14282a (GH, NY). Pinal Co.: Near Oracle, Santa Catalina Mts., *Lewis* 1079 (RSA, UC). Peppersauce Canyon, Santa Catalina Mts., *Darrow in 1937* (NY). Hills near Oracle, *Harrison & Kearney* 6673 (US). 7.7 to 7.9 mi SE of Oracle, Santa Catalina Mts., *Towner* 1, 3 (DS). Santa Cruz Co.: Mustang Mts., *Pringle in 1884* (F, GH, MO, NY, POM, US). Near Sonoita, *Harrison & Kearney* 5713 (ARIZ, US). Sonoita to Elgin, *Peebles & Fulton* 11485 (ARIZ, US). 7.5 mi E of Sonoita, *Gregory* 404, 405 (DAO, RSA, UC). 7.5 mi SE of Sonoita on road to Canelo, *Towner* 105 (DS).

MEXICO. COAHUILA: Santa Rosa Mts., *Marsh* 1338, 1491 (F, OKLA, SMU, TEX). 27 mi E of Boquillas, *Henrickson* 11611b (TEX). 64 mi W of Cuatro Ciénegas, *Henrickson* 7861 (TEX). 4.5 km E of Matrimonio Viejo, *Johnston* 10895 (TEX).

Most abundant of the races of this species, *Calylophus hartwegii* subsp. *pubescens* occurs widely in Texas and neighboring states. In central Texas, it is the only member of sect. *Salpingia*. Spreading trichomes and broad truncate-based leaves are strongly correlated in this form, and are characteristic of the central Texas populations and most others which are not affected by introgression. The type of *Oenothera greggii* is tentatively included here, although the plants are stunted and somewhat lacking in distinctive characters. They are not typical of *C. hartwegii* subsp. *pubescens* and may represent hybrids or introgressants with subsp. *hartwegii*, which also occurs in that region. For these reasons, I have followed Shinners' (1964) decisions and taken up the epithet "*pubescens*" for this taxon.

Calylophus hartwegii subsp. *pubescens* is one of the most variable taxa in *Calylophus*, much of this perhaps stemming from the influence of introgression. The size of the flowers and of leaves and other vegetative parts all vary widely. Leaf margins may or may not be crinkled. Pubescence may consist wholly of spreading hairs or of these combined with shorter glandular or nonglandular pubescence. These characters appear to vary in response to genetic exchange with subspp. *filifolius* and *hartwegii*.

Records of pollinators reported by Gregory (1964; as *Oenothera greggii*) in Terrell Co., Texas and Cochise Co., Arizona, included hawkmoths in the evening at both sites (*Hyles lineata*, *Manduca quinquemaculata*, *Sphinx dolli*) and bees in the morning at the Cochise Co. site (*Megachile*, *Melissodes*, *Bombus*). On a different date at the same locality in Arizona, I observed numerous halictid bees (*Dialictus*, *Agapostemon*, *Evylaeus*) and some bumblebees (*Bombus*) gathering pollen in the late afternoon. In the evening, hawkmoth (*Hyles lineata* and *Manduca quinquemaculata*) visitation was frequent. My field and greenhouse observations showed a range in anthesis times extending from 2 hours before sunset to about sunset. Thus flowers in this subspecies may not always be open early enough for significant afternoon visitation by bees. Ultraviolet-absorbing regions on the petals were found to be of small to moderate size. Each of four plants that were artificially pollinated was found to be self-incompatible.

Tetraploidy and translocation heterozygosity are present in *C. hartwegii* subsp. *pubescens*, with tetraploidy occurring in one (Pecos Co., Texas, *Munz & Gregory* 23405) of the 18 populations which have been examined. A population intermediate between subsp. *pubescens* and subsp. *hartwegii* (Brewster Co., Texas, *Munz & Gregory* 23401) was also found to be tetraploid by Kurabayashi et al. (1962). Interchange heterozygotes comprised 15 of 20 plants examined for meiotic configurations, occurring in 11 of 15 populations. An average of 1.2 translocation heterozygosities per plant was calculated for this form, with a maximum of 3, the most frequent number being 1. No extra diminutive chromosomes have yet been observed in *C. hartwegii* subsp. *pubescens*. Configurations obtained from hybrids with other members of sect. *Salpingia* exhibited 0–2 translocation heterozygosities.

Most instances of introgression have been discussed in earlier sections. Two possible cases of hybridization with *C. lavandulifolius* were discovered for this taxon, perhaps the only subspecies of *C. hartwegii* which hybridizes in nature with *C. lavandulifolius*. One was a sight record from Guadalupe Co., New Mexico, where some plants with slight resemblances to *C. lavandulifolius* were found in two populations of *C. hartwegii* subsp. *pubescens*. The second was a single plant intermediate between the same taxa [between Globe and Cooley(?), Arizona, *Nelson* 10372, (RM)] observed in a mixed collection of the two typical forms. Numerous cases of sympatry without hybridization were observed, especially with *C. serrulatus* in Oklahoma, New Mexico, and the northern Texas Panhandle, and with *C. berlandieri* in central Texas and the Panhandle. Other instances included populations mixed with *C. lavandulifolius* in Culberson Co., Texas and with *C. tubicula* in Chaves Co., New Mexico.

2. ***Calylophus lavandulifolius*** (Torr. & A. Gray) Raven, *Brittonia* 16: 286. 1964.

Oenothera lavandulaefolia Torr. & A. Gray, *Fl. N. Amer.* 1: 501. 1840. *O. hartwegii* Benth. var. *lavandulaefolia* (Torr. & A. Gray) S. Wats., *Proc. Amer. Acad. Arts* 8: 590. 1873. *Galpinsia lavandulaefolia* (Torr. & A. Gray) Small, *Fl. S.E. U.S.* 845, 1335. 1903. *Oenothera hartwegii* var. *fendleri* (A. Gray) A. Gray subvar. *lavandulaefolia* (Torr. & A. Gray) H. Lév., *Monogr. Onoth.* 334. 1908. *O. lavandulaefolia* var. *typica* Munz, *Amer. J. Bot.* 16: 704. 1929. *Calylophus hartwegii* (Benth.) Raven var. *lavandulaefolius* (Torr. & A. Gray) Shinnars, *Sida* 1: 345. 1964. *Oenothera lavandulifolia* var. *lavandulifolia*; Munz, *N. Amer. Fl.*, ser. 2, 5: 138. 1965. *Calylophus hartwegii* subsp. *lavandulifolius* (Torr. & A. Gray) Towner & Raven, *Madroño* 20: 243. 1970.

Oenothera lavandulaefolia Torr. & Gray var. *glandulosa* Munz, *Amer. J. Bot.* 16: 705. 1929. *Galpinsia lavandulaefolia* (Torr. & A. Gray) Small var. *glandulosa* (Munz) Moldenke, *Phytologia* 2: 134. 1946. TYPE: United States, Nevada, White Pine Co., Ely, 30 July 1923, M. E. Jones (POM).

Similar to *Calylophus hartwegii*. Suffrutescent perennial from a stout woody caudex, caespitose, sometimes appearing more or less tufted; stems several to many, moderately branched, spreading-decumbent to more or less ascending, 0.4–2(–3) dm high; plant densely gray-strigulose throughout. Leaves dense on the stem, sessile, usually ascending, linear to narrowly lanceolate or narrowly oblanceolate, 6–50 mm long, 0.8–6 mm wide, the tip acute or obtuse, the base acute-attenuate, the margin entire or nearly so, occasionally slightly undulate, infrequently revolute; small axillary leaves present, 2–10 mm long; lowest stem leaves somewhat wider and more oblanceolate than above. Floral tube 25–60 mm long, 5–15 mm wide at the throat, minutely strigulose or glandular-pubescent without, sometimes with purple longitudinal lines and base, occasionally fading pinkish upon wilting. Sepals 8–20 mm long, 3–8 mm wide, with free tips 0.3–3 mm long, usually with purple marginal stripes. Petals 12–28 mm long, similar in width, usually fading pinkish to purplish, highly ultraviolet-reflective, with a small basal ultraviolet-absorptive spot, rarely medium-sized. Filaments 6–12 mm long; anthers 5–11 mm long. Style 30–75 mm long, glabrous above, minutely pubescent below; stigma 2–5 mm broad; ovary 4–16 mm long, 1–2 mm wide. Capsule 6–25 mm long, 1–3 mm wide; seeds 1.5–2.5 mm long. Self-incompatible. Gametic chromosome number, $n = 7$.

TYPE: UNITED STATES. On plains, probably along the South Platte River in southwestern Nebraska or northeastern Colorado, June or July 1820, *Edwin James* (PH). The approximate locality was taken from McKelvey (1955: 213–219) and is at the eastern limit of the range of this species.

Distribution (Fig. 17): Local and sparse, on sandy and rocky, often calcareous soil, on high plains and in mountains, frequently with *Juniperus*, *Pinus monophylla* or *Pinus edulis*, *Cercocarpus*, *Artemisia tridentata*, occasionally in lower zones with *Larrea divaricata* or in higher zones with *Pinus ponderosa*, from southern Fall River Co., South Dakota, southeastern Wyoming, and far western Nebraska, through western Kansas, Colorado, eastern and southern Utah, northwestern Oklahoma, and the Texas Panhandle to Trans-Pecos Texas, central Nuevo León, central New Mexico, central Arizona, and east-central and southern Nevada. Occurring from elevations of ca. 600 m (2 mi W of Hays, Ellis Co.,

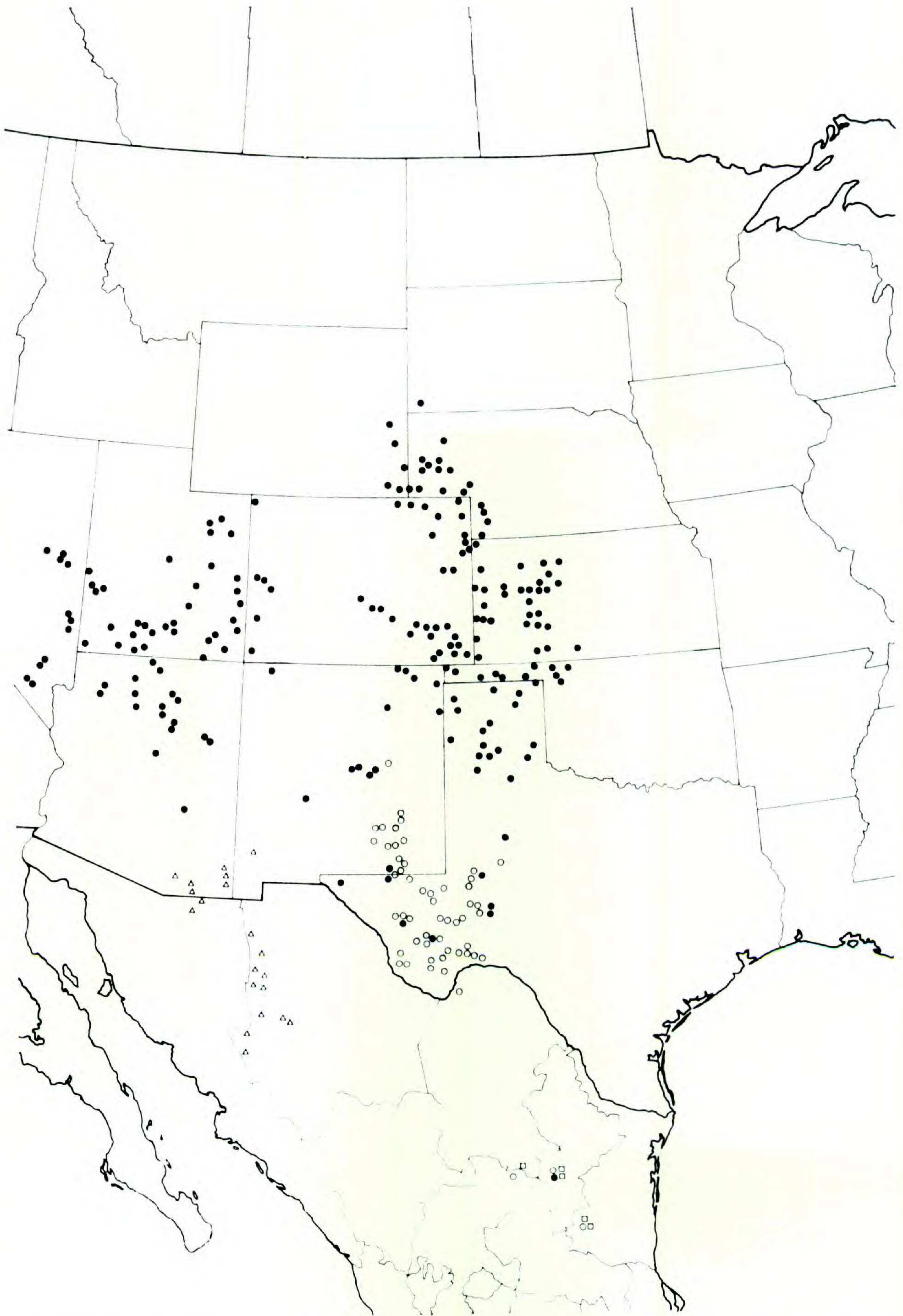


FIGURE 17. Distributions of *Calylophus toumeyi* (triangles), *C. lavandulifolius* (dots), *C. tubicula* subsp. *tubicula* (open circles), and *C. tubicula* subsp. *strigosus* (squares).

Kansas) to ca. 2,750 m (Lee Canyon, Spring Mts., Clark Co., Nevada). Flowers April to August.

Representative specimens examined:

UNITED STATES. SOUTH DAKOTA: Fall River Co.: Rocky dry ridges, *Over 18074* (RM). WYOMING: Goshen Co.: 4 mi N of La Grange, *Stephens & Brooks 22903* (DS). Laramie Co.: Hartville, *Nelson 8328* (GH, MO, NY, US). 20 mi W of Pine Bluffs, *Porter & Porter 8153* (DS, POM, UC). SE edge of Pine Bluffs, *Stephens & Brooks 22873* (DS). Platte Co.: Whalen Canyon, *Nelson 526* (GH, MO, NY, US). Near Guernsey, *Porter 3557* (DS, SMU, TEX, UC, WTU). NEBRASKA: Box Butte Co.: 5 mi E and 5 N of Hemingford, *Stephens & Brooks 24542* (KANU). Chase Co.: 10 mi N of Imperial, *Brown 1255* (NEB). Garden Co.: 2 mi S of Lewellen, *Stephens & Brooks 11519* (KANU). Morrill Co.: Angora, *Pool in 1912* (MO, NEB). 4 mi N of Broadwater, *Stephens & Brooks 13907* (DS, KANU). Scott's Bluff Co.: 1.5 mi W and 5 S of Melbeta, *Stephens 5484* (KANU). COLORADO: Baca Co.: 9 mi S and 2 E of Walsh, *Stephens & Brooks 21820* (DS). Bent Co.: 15 mi SE of Las Animas, *Stephens & Brooks 22003* (DS). 4.5 mi W of Prowers, *Stephens & Brooks 21989* (DS). Dolores Co.: Just W of Northdale, *Anderson 3138* (DS). Huerfano Co.: 19 mi NE of Walsenburg, *Stephens & Brooks 22229* (DS). Kit Carson Co.: 5 mi E of Flagler, *Stephens & Brooks 22633* (DS). Las Animas Co.: 6 mi N and 4 E of Andrix, *Stephens & Brooks 21900* (DS). Otero Co.: 2 mi S of Manzanola, *Stephens & Brooks 22315* (DS). Sedgwick Co.: 1 mi S of Julesburg, *Stephens & Brooks 24060* (KANU). KANSAS: Clark Co.: 8 mi N of Ashland, *Horr E248* (COLO, DAO, F, GH, KANU, LL, OKL, RM, SMU, TEX, UC). Ellis Co.: 2 mi W of Hays, *Bondy 77* (ARIZ, F, MO, NMC, OKL, PH, RM, US). Gove Co.: 20 mi S and 3 E of Oakley, *Lathrop 3374* (KANU, SMU). Meade Co.: 12 mi E of Meade, *Horr 3532* (KANU, TEX, US). Morton Co.: 7 mi N and 4 W of Elkhart, *Stephens 8877* (KANU). Scott Co.: Horsethief Canyon, Scott County State Park, *Fearing & Latham in 1950* (GH, KANU). Trego Co.: 14 mi S of Ogallah, *McGregor 17124* (KANU). OKLAHOMA: Beaver Co.: E edge of Elmwood, *Stephens & Brooks 21745* (DS). Harper Co.: 10 mi S of Buffalo, *Goodman 2394* (MO, NY, OKL, POM, UC, WTU). Texas Co.: 5.5 mi E of Hardesty, *Stephens & Brooks 21776* (DS). Woods Co.: Near Freedom, *Stevens 252* (DS, GH, NY, OKL, SMU). TEXAS: Brewster Co.: Foothills of Glass Mts., 7.7 mi NE of U.S. 90 on U.S. 67, *Towner 29* (DS). Culberson Co.: 25.6 mi SW of White's City, E side of Guadalupe Mts., *Towner 24* (DS). Hudspeth Co.: 31 mi E of El Paso, Hueco Mts., *Tharp 46071* (F, MO, TEX). NEW MEXICO: Colfax Co.: Near Raton, *Nelson & Nelson 4681* (DS, RM, US). Eddy Co.: Near Three Forks of Rocky Arroyo, Guadalupe Mts., *Wilkins 1711* (PH). Socorro Co.: Hell Canyon, Magdalena Mts., *Herrick 274* (US). Torrance Co.: 3.0 mi NE of Duran, *Raven 19129* (DS). 5.8 mi SW of Duran, *Raven 19133* (DS). Ca. 7.5 mi W of Willard on U.S. 60, *Towner 120* (DS). ARIZONA: Coconino Co.: Rim of Canyon Diablo, Two Guns, *Demaree 44216* (ARIZ, PH, RSA, SMU). E rim of Canyon Diablo, Two Guns, *Towner 114* (DS). 10 mi SE of Tuba City, *Peebles 13363* (GH, US). 10.9 mi S of Bitter Springs, *Mosquin & Mosquin 4247* (DS). Mojave Co.: Ca. 1 mi from rim of canyon, Toroweap Valley, *McClintock 52-512* (ARIZ, NY). Navajo Co.: 45.0 mi NW of Concho, *Towner 115* (DS). UTAH: Duchesne Co.: Juniper zone, below Moon Lake, *Graham 6412* (MO, POM). Emery Co.: 50 mi N of Hanksville, San Rafael Swell, *Cronquist 9201* (DAO, DS, NY, POM, WTU). Garfield Co.: Red Canyon, 10 mi W of Bryce Canyon, *Preece 2480* (COLO, POM, SMU). Bryce Canyon, *Goodman & Hitchcock 1566* (DS, GH, POM, RM, UC). 10 mi E of Escalante, *Holmgren & Nielsen 7734* (DS, POM, RM, UC, WTU). Millard Co.: Tunnel Springs, Desert Game Range, *Cottam 8553* (ARIZ, POM). San Juan Co.: Tuwa Canyon, Natural Bridges National Monument, *Welsh & Moore 2294* (NY). Uinta Co.: Willow Creek, S of Ouray, *Holmgren 1882* (KANU, WTU). Washington Co.: 10 mi N of the Beaver Dam summit of U.S. 91 and 5 mi NW of the highway, *Wiens 3917* (WTU). NEVADA: Clark Co.: Old Saw Mill site, Sheep Mts., 6,600 ft, *Alexander & Kellogg 1757* (GH, UC, US, WTU). Rocky ridge S of Deer Creek, Charleston (Spring) Mts., 2,670 m, *Clokey & Clokey 7605* (ARIZ, CAN, COLO, DAO, DS, F, GH, KANU, MO, OKL, PH, POM, RM, RSA, SMU, TEX, UC, US, WTU). 4.8 mi N of Kyle Canyon on road to Lee Canyon, Charleston Mts., *Towner 101* (DS). Lee Canyon, 0.7 mi W of jct. to Kyle Canyon, Charleston Mts., *Towner 104* (DS). Lincoln Co.: Panaca Valley and vicinity, *Gentry 131* (ARIZ, DS, UC, US). White Pine Co.: 3 mi S of Ruth, *Moore 346* (DS, POM). 5.1 mi S of U.S. 50, on eastern road to Hamilton, *Raven & Solbrig 13550* (DS). 2 mi W of Ely, *Anderson 2897* (KSC). MEXICO. NUEVO LEÓN: 15 mi S of San Roberto Junction on Mexico 57, *Sanderson 291, 292* (TEX); *Turner 6357* (TEX). 16 mi S of San Roberto Junction, *Reveal et al. 2652* (DS). Near summit of N.L. Highway 60 W of Galeana, *Sanderson 288*, in part (TEX).

The limits of this species are approximately those given by Munz (1929). Some collections included here by Munz clearly belong with *Calylophus hartwegii* subsp. *hartwegii*, e.g., Zacatecas, gravelly soil, *Purpus* in 1903 (UC). The two taxa are easily confused but differ in the shorter sepal tips, denser pubescence, and leaves which are usually broader and obtuse-tipped in *C. lavandulifolius*.

A species of broad distribution, *C. lavandulifolius* occurs for the most part to the north and northwest of the range of *C. hartwegii*. Isolated collections have been made, however, throughout much of the range of the latter. Where *C. lavandulifolius* occurs with *C. hartwegii*, it tends to occupy higher elevations than any race of that species, except for *C. hartwegii* subsp. *fendleri*. Plants of *C. lavandulifolius* are typically slow-growing, small, and sparsely distributed, and are relatively inconspicuous when mixed with populations of the more abundant *C. hartwegii*.

Hybridization with other species of *Calylophus* apparently occurs only rarely. Evidence for gene exchange stems only from the two collections mentioned previously which were intermediate between *C. lavandulifolius* and *C. hartwegii* subsp. *pubescens*. Instances of populations of *C. lavandulifolius* contiguous with those of other taxa have also been mentioned above, and include contact with *C. tubicula* subsp. *tubicula*, *C. tubicula* subsp. *strigulosus*, *C. hartwegii* subsp. *pubescens*, *C. hartwegii* subsp. *fendleri*, and *C. serrulatus*.

Variation within *C. lavandulifolius* is not clearly correlated with geography, and division into subspecies seems inadvisable. The glandular pubescence of the floral tube and calyx used by Munz to distinguish *Oenothera lavandulaefolia* var. *glandulosa* does not appear to vary in any meaningful pattern or in association with any other character. Considerable variation within the species occurs in leaf dimensions, leaf margin (undulate, revolute, or plane), width of the floral tube, and in other floral characters.

Visitors to a population in Clark Co., Nevada (*Towner 195*) consisted entirely of hawkmoths (*Hyles lineata*, *Manduca*), which were active between dusk and dark. Anthophorid and halictid (*Agapostemon*) bees were seen on flowers 2 hours before sunset at a population in Torrance Co., New Mexico (*Towner 120*). Anthesis in the field and greenhouse ranged from 3 hours before sunset to sunset. In the population in Clark Co., Nevada the median time of anthesis was 1½ hours before sunset. Ultraviolet absorption patterns on the petals tend to be small in this species. The foregoing facts suggest that hawkmoth pollination predominates in *C. lavandulifolius*, but that bees may also play a role at certain localities. Two plants were self-pollinated and found to be self-sterile.

Cytological variation in *Calylophus lavandulifolius* occurs in the form of translocations and extra diminutive chromosomes. Seven of 10 plants from 5 of 6 populations were interchange heterozygotes. An average of 1.2 heterozygosities per plant was calculated. Three individuals from separate populations had extra chromosomes, which consisted of 1 or 2 diminutive pairs. Configurations displayed by hybrids of *C. lavandulifolius* with other taxa in sect. *Salpingia* showed 2-3 translocation differences and occasional inversion differences between the

parents, a greater cytological divergence than shown by other crosses within the section.

3. ***Calylophus toumeyi*** (Small) Towner, comb. nov.—FIGS. 1, 3.

Galpinsia toumeyi Small, Bull. Torrey Bot. Club 25: 317. 1898. *Oenothera hartwegii* Benth. var. *toumeyi* (Small) Munz, Amer. J. Bot. 16: 708. 1929. *O. toumeyi* (Small) Tidestrom, Proc. Biol. Soc. Wash. 48: 41. 1935. *Calylophus hartwegii* (Benth.) Raven var. *toumeyi* (Small) Shinnars, Sida 1: 341. 1964. *C. hartwegii* subsp. *toumeyi* (Small) Towner & Raven, Madroño 20: 243. 1970.

Similar to *Calylophus hartwegii*. Suffrutescent perennial from a stout woody caudex; stems several, sparingly branched or unbranched above, ascending to erect, 1.5–6(+) dm high; plant subglabrous to minutely strigulose throughout. Leaves sparsely distributed on the stem, sessile, more or less spreading, narrowly lanceolate, 10–35 mm long, 1–7 mm wide, the tip acute, the base acute-attenuate, the margin entire to obscurely and sparsely serrulate, not undulate; conspicuous fascicles of small leaves 2–25 mm long in nonfloriferous axils; lowest stem leaves usually tending towards oblanceolate shape. Floral tube (15–)30–60(–70) mm long, 5–14 mm wide at the throat, yellowish, fading orangish to brick red upon wilting. Sepals 10–25 mm long, 3.5–6 mm wide, with free tips 2–9(–12) mm long, colored as the floral tube. Petals 10–20 mm long, similar in width, intensely lemon yellow, fading orangish to brick red, moderately ultraviolet-absorptive throughout. Filaments 4–12 mm long; anthers 6–10 mm long. Style 35–70(–80) mm long, glabrous above, minutely pubescent below; stigma discoid to squarish, 1.5–4 mm broad; ovary 6–20 mm long, 1–2 mm wide. Capsule 10–50 mm long, 1.5–4 mm wide, thin walled, sometimes almost papery, dehiscent only in the distal half; seeds 2–3 mm long. Self-incompatible. Gametic chromosome number, $n = 7$.

TYPE: UNITED STATES. ARIZONA: Cochise Co., Chiricahua Mountains, 25 July 1894, *J. W. Toumey 197* (NY); Munz, Amer. J. Bot. 16: 708. 1929.

Distribution (Fig. 17): Local and uncommon on shaded rocky slopes or disturbed areas in pine-oak forest, from the Santa Rita, Huachuca, and Chiricahua mts. in Santa Cruz and Cochise cos., Arizona, and the Mogollon Mts. in southern Catron Co., New Mexico, south through northeastern Sonora in the Sierra Madre Occidental to west-central Chihuahua. From elevations of ca. 1,500 m (Stone Cabin Canyon, Huachuca Mts., Santa Cruz Co., Arizona) to 2,600 m (summit of the José Mts., Sonora). Flowers mostly from July to October, but some populations in Mexico as early as May.

Representative specimens examined:

UNITED STATES. NEW MEXICO: Catron Co.: On or near the West Fork of the Gila R., Mogollon Mts., *Metcalf 555* (ARIZ, GH, MO, NMC, US). ARIZONA: Cochise Co.: Huachuca Mts., *Harrison & Kearney 5773* (US). Fort Huachuca, *Wilcox in 1892* (NY). Near Fort Huachuca, *Wilcox 253* (US). Huachuca Mts., 7000 ft, *Jones in 1903* (DS, POM, US). Huachuca Mts., *Toumey in 1894* (GH, RM, US). Tanner's Canyon, Huachuca Mts., *Gilbert in 1892* (NY). Tanner's Canyon, Huachuca Mts., *Lemmon in 1882* (UC). Ramsey's Canyon, Huachuca Mts., *Goodding 786* (RM, US). Miller Canyon, Huachuca Mts., *Carter in 1936* (NMC). Carr Peak, Huachuca Mts., 6500 ft, *Benson 10500* (POM). Carr Peak, Huachuca Mts., *Goodding 222* (ARIZ, GH, NEB, NY, OKLA, RM). 5.6 mi up Carr Canyon road from Arizona 92, Huachuca Mts., *Towner 106* (DS). Reef Mine, Huachuca Mts., 7100 ft, *Gould*

1475 (ARIZ, UC). Garden Canyon, Huachuca Mts., *Harrison & Kearney 5773* (ARIZ). Near Fort Huachuca, Huachuca Mts., *Lemmon 2700* (GH). Rucker Canyon, upper left fork, Chiricahua Mts., *Blumer 2025* (F). Sugar Loaf Mt., Chiricahua Mts., *Darrow in 1937* (ARIZ). N slope of Sugar Loaf, Chiricahua National Monument, *Clark 8280* (ARIZ). Sugarloaf Trail just below tunnel, Chiricahua National Monument, *Towner 107* (DS). Near summit of pass, Chiricahua Mts., *Goodding 165-47* (ARIZ). Pine Canyon, Chiricahua Mts., 6700 ft, *Blumer 1610* (ARIZ, DS, F, MO, NEB, NMC, NY, RM, US). Ida Peak, along Telephone Trail, Chiricahua Mts., 8,000 ft, *Stone 517* (PH, RM). Pinery Canyon, Chiricahua Mts., 7,000 ft, *Barr 64-353* (ARIZ). 12.4 mi W of jct. of Arizona 186 & 181, in Pinery Canyon, Chiricahua Mts., ca. 7,000 ft, *Towner 164* (DS). 12.5 mi W of jct. Arizona 186 & 181, *Towner 171*. 1 mi below Onion Saddle, E. side of Chiricahua Mts., *Kaiser 49-209* (ARIZ). Crest Trail, Chiricahua Mts., 7,000 ft, *Hernbrode 136* (ARIZ). Gut Saw Canyon, Chiricahua Mts., *Goodding 2339* (UC). Wonderland of Rocks, Chiricahua Mts., *Darrow in 1937* (GH, NY). Bonita Canyon, Chiricahua Mts., *Henderson in 1933* (TEX). Outlaw Canyon, Chiricahua Mts., *Goodding 2339* (RM). Pima Co. (?): Sabino Canyon, Catalina Mts., 3,000 ft, *Jones in 1903* (MO, specimen immature; either not of this species or locality incorrect). Santa Cruz Co.: Madera Canyon, Santa Rita Mts., 5,900 ft, *Darrow 2614* (ARIZ). Madera Canyon, Santa Rita Mts., *Peebles et al. 4545* (ARIZ, US). Stone Cabin Canyon, Santa Rita Mts., 5,000 ft, *Thornber in 1903* (ARIZ). Santa Rita Mts., 6,000–8,000 ft, *Pringle in 1881* (F, GH). Santa Rita Mts., 7,000 ft, *Darrow & Arnold in 1936* (MO, OKL). Upper Madera Canyon, Santa Rita Mts., *Clark 12351* (GH, OKL). Along trail from Mount Wrightson to White House Canyon, Santa Rita Mts., 7,000 ft, *Parker et al. 5835* (ARIZ, NY).

MEXICO. SONORA: Puerto de los Aserrados, region of the Río de Bavispe, *White 3190* (ARIZ). Summit of the José Mts., 8,600 ft, *Mearns 1606* (DS, US). Cananea, *Murdoch in 1914* (F). CHIHUAHUA: 48 mi W of Matachic on road to Ocampo, 8,400 ft, *Wiens 3445* (COLO, DS). Mojarachic (Maguarachic?), *Knobloch 5094* (F). Mts. NW of Chihuahua, *Le Sueur in 1936* (MO, TEX, UC, US). San José de Pinal, Río Mayo, 7,000 ft, *Gentry 2587* (ARIZ, F, MO, POM, UC, US). Mts. SW of Chichuichupa, *Hartman 712* (F, NY, UC, US). Mexican NW railroad, km 85, *Barlow in 1911* (F). Ridge between Río Chico and Río Caballo, Mexican NW railroad, Continental Divide, *Barlow in 1911* (F). Carretas, *White 993* (ARIZ). 130 mi W of Chihuahua City, 8,500 ft, *Russell in 1957* (UC). Cañon Huahuatán, 10 mi SE of Madera, *Muller 3428* (UC). Guayanopa Canyon, Sierra Madre, *Jones in 1903* (POM). Salto de Babicora, *Le Sueur 1407* (F). W from Pearson (now Juan Mata Ortiz), Sierra Madre, *Barlow in 1911* (F). Sierra Madre, *Nelson 6088* (US). No specific locality, *Le Sueur 101* (F, TEX).

This most distinct of the large-flowered members of sect. *Salpingia* is readily separated using any of several characters, including its exclusively montane distribution, fascicles of large axillary leaves, tall erect stems, long sepal tips, partially dehiscent capsule, and unusual ultraviolet absorption pattern on the petals. Apparently completely allopatric to the other taxa of sect. *Salpingia*, *Calylophus toumeyii* experiences no current genetic exchange with them. The absence of any intermediate collections and the number of characters which show discontinuities from *C. hartwegii* indicate the validity of specific status for *C. toumeyii*, which was not recognized in an earlier publication (Towner & Raven, 1970).

Distributed in the mountains of southeastern Arizona, southwestern New Mexico, and northeastern Mexico, this species is physically and ecologically separated from other members of sect. *Salpingia*. The blooming period is unusual for the genus, occurring in late summer and early fall in response to summer rainfall. Earlier flowering is prevented by the late, dry spring, characteristic of montane areas in this region.

Flower visitation to *C. toumeyii* seems sporadic, as insects were seen only once in significant numbers during several attempted studies. On that occasion, in the Chiricahua Mts., of Arizona (*Towner 238*), bees of the genus *Lasioglossum* were active gathering pollen shortly before dusk, and again after sunrise. Hawk-

moths were abundant visitors in the evening. Morphological characters and anthesis times suggest that hawkmoths are the principal pollen vectors. The floral tube attains a length of 70 mm in some specimens, the maximum seen in *Calylophus*, and is perhaps a response to pollination by the genera of sphingids with longer tongues (cf. Gregory, 1964). Moderately absorptive to ultraviolet light over their entire area, the petals have no contrast pattern, nor do they contrast with vegetative parts (Fig. 12). Anthesis occurs $\frac{1}{2}$ to $1\frac{1}{2}$ hours before sunset. Bees are therefore not likely to be regular and significant contributors to pollination.

Self-incompatibility is probably typical for this species. Only one plant was checked by self-pollination, and it was self-sterile. In one field study, a population was observed to have set no seed in spite of having been in flower for several weeks. The same population showed over 60% fertile capsules on the date of the cited pollination study.

Three plants from two Arizona populations were examined cytologically and proved to be heterozygous for two translocations apiece. Multivalent associations included a ring of 6 chromosomes in 1 plant and 2 rings of 4 chromosomes in the 2 others. One of each type of configuration was found in a population from the Chiricahua Mountains (*Towner 107*), indicating that at least 3 translocation polymorphisms were present in the population. Chromosome determinations from hybrids were not obtained because of the difficulty of crossing *C. toumeyii* and *C. hartwegii* and because of the scarcity of floral buds on those hybrids which were produced.

4. *Calylophus tubicula* (A. Gray) Raven, Brittonia 16: 286. 1964.

Oenothera tubicula A. Gray, Pl. Wright. 1: 71. 1852.

Herbaceous or slightly suffrutescent short-lived perennial, arising from a slender woody caudex; stems one to several, sparingly branched above, subdecumbent-ascending to nearly erect, 0.4–5.3 dm high; plant with short glandular pubescence throughout, or with some parts minutely strigulose. Leaves \pm dense, subsessile, ascending, linear to ovate or obovate, 7–46 mm long, 0.7–11 mm wide, the tip acute, sometimes obtuse in lowermost leaves, the base acute-attenuate, the margin entire or sparsely and shallowly serrulate, occasionally slightly undulate; fascicles of small leaves 2–15 mm long in nonfloriferous axils; lowest stem leaves more frequently oblanceolate than above. Inflorescence dense, with buds crowded near the stem apex; buds terete. Floral tube funnellform in upper one-half or more, often tubular below, 5–25(–33) mm long, 3–10 mm wide at the throat in pressed specimens, the inner surface glabrous above to densely pubescent basally, yellow, sometimes fading pink, and more rarely, purplish. Sepals 3–13 mm long, 2–6 mm wide, with subulate free tips 0.5–2 mm long, plane, yellow, rarely with purple marginal stripes, only infrequently fading pink or purplish. Petals suborbicular to obovate-truncate, 5–20(–25) mm long, similar in width, infrequently fading pink to purplish, highly ultraviolet-reflective, with a large basal ultraviolet-absorptive spot. Stamens subequal; filaments 1–6 mm long, glabrous to minutely pubescent; anthers 2–7 mm long, sparsely and minutely

pubescent. Style 9–30(–40) mm long, usually exceeding the stamens, glabrous above, minutely pubescent below; stigma discoid to squarish, 1–2.5 mm broad; ovary 4–11 mm long, 0.5–1.5 mm wide. Capsule 8–19 mm long, 1.5–2.5 mm wide, moderately thin walled, completely dehiscent; seeds 1.0–1.4 mm long, obovoid, angled, truncate at the apex. Self-incompatible. Gametic chromosome number, $n = 7$.

TYPE: UNITED STATES. TEXAS: prairies beyond the Pecos River, probably in eastern Pecos Co., August 1849, *Charles Wright 197* (in part = 821; GH).

Distribution (Fig. 17): Primarily on limestone soils in arid lowlands, but occasionally in montane areas, from Guadalupe Co., New Mexico, south to western Texas, thence northeast to Howard Co., Texas and south to northern Zacatecas, south-central Nuevo León, and southwestern Tamaulipas. From ca. 600–1,800 m elevation. Flowers April to August.

Cytological relationships, interfertility, and a number of morphological characters demonstrate a close affinity between *Calylophus tubicula* and the other members of sect. *Salpingia*. However, the short-tubed, funnelform flowers (Fig. 4) and morning anthesis of this species constitute a phenetic similarity to sect. *Calylophus*, a relationship likely due to evolutionary convergence. *Calylophus tubicula* is distinguished from its closest relatives by those same characters. In addition, individuals of this species are shorter-lived than in other forms in the section. The plants rarely have large taproots, and are difficult to maintain for more than one or two years in cultivation.

Self-sterility was found in six plants from two populations of *C. tubicula* subsp. *tubicula*, and no evidence of self-compatibility was seen in any cultivated or wild plants of either subspecies. Stigmas were invariably well exerted and no greenhouse specimens of either subspecies ever set seed spontaneously. Anthesis occurred just before dawn ($\frac{1}{2}$ to $1\frac{1}{2}$ hours before sunrise) at two colonies of *C. tubicula* subsp. *tubicula* in Eddy Co., New Mexico and in cultivated representatives of both subspecies. Stamens, the stigma, and a large spot at the base of each petal are ultraviolet-absorptive, contrasting markedly with the rest of the petal surface, which is highly reflective.

Flower visitors at field sites (*Towner 14, 15*) of *C. tubicula* subsp. *tubicula* consisted primarily of small halictid bees of several genera, especially *Evyllaenus*, *Dialictus*, and *Agapostemon*. These were most active from just before sunrise to mid-morning, gathering both pollen and nectar. Infrequent visits by hawkmoths (*Hyles lineata*) were observed shortly before sunrise. In some colonies, removal of pollen was virtually complete by afternoon. Field data, anthesis times, and flower morphology indicate that this species is predominantly bee-pollinated. A strong inference can be made that *C. tubicula* evolved from a moth-pollinated ancestor resembling *C. hartwegii*. This is based on the relatively long floral tubes in some *C. tubicula* and on the close phenetic and cytogenetic relationship of the two species.

Relative to other forms of *Calylophus*, *C. tubicula* has a low level of chromosome heterozygosity. Eight of 14 plants examined had multivalents, and no evidence of inversions, diminutive chromosomes, or polyploidy was found. The

average number of observable translocation heterozygosities per plant was 0.7, as compared with 1.0 for the rest of sect. *Salpingia* and 1.9 for *C. berlandieri*.

Individuals from certain populations of *C. tubicula* may approach or exceed the minimum floral tube length seen in *C. hartwegii*. In such cases, *C. tubicula* generally retains the wider funnelform shape of the tube. Other populations show vegetative characteristics which suggest recent introgression with or derivation from *C. hartwegii*. These cases will be discussed under the subspecies.

Differences of pubescence, leaf shape, floral pigments, and ecological distribution distinguish the two subspecies listed below. The extremes of each form are quite distinct, but individuals from several collections in Mexico cannot be assigned with certainty to either taxon.

KEY TO SUBSPECIES

- a. Glandular-pubescent throughout; leaves narrowly lanceolate to ovate; flowers rarely fading reddish or purple 4a. subsp. *tubicula*
 aa. Minutely grey-strigulose on the ovary and upper stems; leaves linear to narrowly lanceolate; flowers commonly fading reddish or purple 4b. subsp. *strigulosus*

4a. *Calylophus tubicula* (A. Gray) Raven subsp. *tubicula*.—FIG. 4.

Galpinsia tubicula (A. Gray) Small, Bull. Torrey Bot. Club 23: 186. 1896. *Oenothera hartwegii* Benth. var. *tubicula* (A. Gray) H. Lév., Monogr. Onoth. 335. 1908.

Oenothera tubicula A. Gray var. *demissa* A. Gray, Pl. Wright. 1: 71. 1852. TYPE: United States, Texas, Culberson Co., on the Guadalupe Mts., October 1849, *Charles Wright 197*, in part = 13380 (GH, holotype; US, isotype). The collection probably came from Texas and not New Mexico (McKelvey, 1955: 1070).

Oenothera × *serrulatoides* H. Lév., Monogr. Onoth. 335. 1908. TYPE: United States, Texas, Pecos Co., valley of the Pecos and towards the Limpio, June 1851, *Charles Wright 1077* (MO, holotype; GH, NY, PH, isotypes). Remark on type sheet: "mais hybride de *tubicula* × *serrulata*?"

Galpinsia glandulifera A. Nels., Amer. J. Bot. 21: 575. 1934. TYPE: United States, New Mexico, Eddy Co., sandy hillsides, vicinity of Carlsbad Caverns, May 1930, *Gladys Convis 36* (RM). Published erroneously as 37.

Galpinsia carlsbadiana A. Nels., Amer. J. Bot. 23: 269. 1936. TYPE: United States, New Mexico, Eddy Co., near the Caverns, Carlsbad National Park, 24 May 1931, *Aven Nelson 11396* (RM, holotype; DS, NY, POM, isotypes).

With short glandular pubescence throughout. Leaves narrowly lanceolate to ovate or obovate, 7–46 mm long, 0.7–11 mm wide, usually entire or nearly so. Flowers rarely fading reddish or purplish upon wilting. Self-incompatible. Gametic chromosome number, $n = 7$.

Distribution (Fig. 17): Colonial, primarily on limestone soils, in flat arid grasslands, often with *Larrea divaricata* and *Yucca*, from Guadalupe Co., New Mexico, south in the western side of the Pecos River drainage to western Texas, where occurring from Culberson Co. east to Howard Co., thence south through Presidio, Brewster, and Terrell cos., and probably most of central Coahuila, to northern Zacatecas, southwestern Nuevo León, and southwestern Tamaulipas. Elevational distribution from ca. 600 m (10 mi E of Dryden, Terrell Co., Texas) to ca. 1,400 m (between Santa Rosa and Vaughn, Guadalupe Co., New Mexico). Flowers April to August.

Representative specimens examined:

UNITED STATES. NEW MEXICO: Chaves Co.: Ca. 4 mi N of Roswell, *Towner 127* (DS). Eddy Co.: 4 mi W of Hope, *Munz & Gregory 23350* (RSA). Memorial Hospital, N end of Carlsbad, *Munz & Gregory 23353, 23354, 23356* (RSA, UC). 0.6 mi W of Hope, *Towner 14* (DS). 1.7 mi NE of Hope, *Towner 16* (DS). Ca. 4.5 mi S of Carlsbad, *Towner 17* (progeny only, DS). 7.6 mi NE of White's City, *Towner 18* (DS). Otero Co.: Ca. 5 mi W of Elk (1 plant), *Towner 108* (DS). TEXAS: Brewster Co.: 41 mi S of Alpine, *Anderson 3030* (DS). Flats near Old Blue, Glass Mts., *Warnock W524* (DS, POM, TEX). 15 mi E of Marathon, *Munz & Gregory 23400* (RSA, UC). Ca. 10 mi E of Alpine, *Sperry T1095* (UC, US). 6 mi S of Marathon, *Rollins & Chambers 2766* (DS, GH, POM, RM, UC). Culberson Co.: 3 mi SW of New Mexico line on U.S. 180, *Munz & Gregory 23360* (RSA). 9 mi E of Van Horn, *Waterfall 4162* (ARIZ, GH, MO, NY). Ector Co.: W of Odessa, *Lundell & Lundell 16921* (LL). Jeff Davis Co.: 8 mi S of Fort Stockton, *Munz & Gregory 22385* (RSA, UC). Pecos Co.: "Mesa slope," *Tharp 43-731* (OKL, OKLA, RM, TEX, CC). Ca. 20 mi W of Sanderson, *Warnock & McBryde 14904* (LL, TEX). 11 mi E of Fort Stockton, *Warnock 5164* (LL, SMU). 30 mi NE of Fort Stockton, *Ownbey & Ownbey 1625* (MO, POM, RM, RSA, UC). Presidio Co.: Up to divide between Long Draw and Capote Draw on road from Marfa to Ruidosa, *Hinckley* (NY, SMU). Cleveland Ranch, near Chinati Mts., *Hinckley* (GH, NY). 5 mi N of Marfa, *Munz & Gregory 23389* (RSA, UC). Reeves Co.: On U.S. 80, 3 mi E of intersection with U.S. 290, *Munz & Gregory 23370, 23371, 23372* (RSA, UC, WTU). On U.S. 80, 1 mi E of intersection with U.S. 290, N edge of the Davis Mts., *Waterfall in 1943* (GH, MO, NY). Plains W of Pecos, *Tracy & Earle 144* (F, GH, MO, NEB, NY, TEX). Terrell Co.: 10 mi E of Dryden, *Parks et al. 56* (TEX). Upton Co.: 20 mi SE of Crane, *Raven & Gregory 19240*. Val Verde Co.: Pumpville, *Fisher 290* (US). Ward Co.: N of Pyote, *Lundell & Lundell 11379* (POM, SMU).

MEXICO. ZACATECAS: 18 km W of Concepción del Oro, *Stanford et al. 590* (DS, MO, NY). SAN LUIS POTOSÍ(?): "Prov. de San Luis," *Octoust 1050* (P).

This subspecies occurs primarily on arid calcareous flats and outcrops in southeastern New Mexico and western Texas. Its distribution in northern Mexico is very poorly known, and may include much of Coahuila in addition to the localities listed. In southern New Mexico, it occurs in the Pecos River Valley and on the plains to the west of it. Other taxa of *Calylophus* supplant *C. tubicula* on the higher plains to the east of the river (the "Llano Estacado").

The broader leaves and glandular pubescence are the primary characters differentiating *C. tubicula* subsp. *tubicula* and *strigulosus* from one another. Introgression between the two seems to occur in Nuevo León, Tamaulipas, and Coahuila. Intermediate specimens are cited under subsp. *strigulosus*.

Twelve plants from 9 populations have been examined during meiosis; 6 had 5 bivalents and a ring of 4 apiece, while 6 had 7 bivalents. Experimental hybrids were obtained with difficulty between *C. tubicula* subsp. *tubicula* and *C. berlandieri* subsp. *berlandieri*. These plants were weak and essentially sterile (0–1% pollen fertility). They showed low chiasma frequency and gave evidence of at least 6 major translocation differences between the forms. Crosses of *C. tubicula* subsp. *tubicula* with other members of sect. *Salpingia* produced progeny which were structurally homozygous or heterozygous for 1 or 2 translocations. Such crosses produced good seed set and reasonably fertile hybrids, although the hybrids frequently showed poor germination and viability.

Introgression between this subspecies and *C. hartwegii* subsp. *fendleri* has been imputed by Munz (1965). Actually, considerable differences in elevational distribution separate *C. hartwegii* subsp. *fendleri* and *C. tubicula* subsp. *tubicula*, the former occurring from ca. 1,500 to 2,150 m elevation in New Mexico. This should make contact between these taxa infrequent. In the Carlsbad Caverns

area, individuals with broad leaves and long floral tubes have been treated as a distinct taxon, *Galpinsia carlsbadiana*, and as possible hybrids between the forms mentioned above. The latter possibility seems remote, since I have discovered no records of *C. hartwegii* subsp. *fendleri* within 160 km of the Caverns area. Taxonomic recognition is unwarranted also for the reason that the long-tubed forms occur together with typical *C. tubicula* in many populations throughout the range of subsp. *tubicula*. It is uncertain whether this pattern should be interpreted as a result of present or past genetic exchange or as spontaneous variation within *C. tubicula*. Collections of *C. tubicula* subsp. *tubicula* showing long floral tubes include the following: 4 mi N of Carlsbad Caverns, Eddy Co., New Mexico, *Porter & Porter 8986* (DS, RM; of all collections, this is the most hybrid-like, being very similar to *C. hartwegii* subsp. *fendleri*). 45 mi S of Pecos, Pecos Co., Texas, *Moore & Moore 21* (NY, SMU, UC). 1–5 mi NW of Notrees, Ector Co., Texas, *Collins 82* (OKLA). Borrow pits N of Pecos, Reeves Co., Texas, *Nelson & Nelson 4989* (DS, MO, RM, TEX, UC, US).

In general, *C. tubicula* subsp. *tubicula* was not found growing together with other forms of *Calylophus*, perhaps because of its restriction to xeric sites at low elevations. In Chaves Co., New Mexico, two individuals of *C. hartwegii* subsp. *pubescens* (*Towner 126*) were found in a large population of *C. tubicula* (*Towner 127*), but with no evidence of hybrids. Likewise, no hybrids were apparent in a situation near the Glass Mountains in Brewster Co., Texas, where *C. tubicula*, *C. lavandulifolius*, and *C. hartwegii* subsp. *pubescens* were all discovered within a 0.3 mile stretch of graded roadside. To the north of Roswell, New Mexico, *C. tubicula* was observed growing within a few miles of *C. hartwegii* subsp. *filifolius* in apparently identical habitats. It can be inferred that these two taxa occasionally come into contact. Their similarity in pubescence might well be a result of some past genetic exchange, although I have seen no signs of current hybridization.

4b. *Calylophus tubicula* subsp. *strigulosus* Towner, subsp. nov.

Differt a subsp. *tubicula* ovario et caulibus superis minute strigulosis, foliis linearibus vel anguste lanceolatis, et floribus plerumque rubescentibus vel purpurascensibus.

Minutely grayish-strigulose on the ovary and upper stems, sometimes throughout, glandular pubescence generally absent. Leaves linear to narrowly lanceolate, 10–35 mm long, 0.8–3 mm wide, often shallowly serrulate. Flowers commonly fading reddish to purple. Self-incompatible. Gametic chromosome number, $n = 7$.

TYPE: MEXICO. NUEVO LEÓN: Along Highway 60, 2 mi W of Galeana Jct., dry rocky open range, 1,700 m, 5 July 1963, *McGregor, Harms, Robinson, del Rosario, & Segal 119* (DS-504949, holotype; KANU, SMU, isotypes).

Distribution (Fig. 17): Uncommon in rocky open sites and canyons in relatively dry montane areas, sometimes in pine forest; southernmost Coahuila, south-central Nuevo León, and southeastern Tamaulipas. From ca. 1,500 to 2,300 m elevation. Records of flowering include July and August.

Representative specimens examined:

MEXICO. NUEVO LEÓN: 15 mi SW of Galeana, *Mueller & Mueller 464* (F, TEX). Hacienda

Pablillo, Galeana, *Taylor 68* (ARIZ, DS, MO, NY, TEX, UC). On canyon wall, 5,400 ft, municipality of Galeana, *Chase 7745* (ARIZ, F, MO, NY). Ca. 35 mi S of Galeana towards Ascención, *Straw & Forman 1374* (RSA). Near summit of Nuevo León Highway 60 W of Galeana, *Sanderson 287, 288* in part (TEX). COAHUILA: SE of Saltillo, *Clark 6710* (MO). Fraile, 59 km S of Saltillo, *Stanford et al. 242* (DS, MO, NY, UC). TAMAULIPAS: 3 mi N of Miquihuana, *Stanford et al. 2472* (DS, NY, RSA, WTU). Jaumave Valley, *Nelson 4461* (US).

The ecological distribution of *Calylophus tubicula* subsp. *strigosus*, which occurs in montane areas of northeastern Mexico, often with pines, contrasts sharply with that of subsp. *tubicula*. The feature in common between the two distributions is perhaps aridity, although the Mexican sites would appear to be more mesic.

Several collections assigned to this subspecies show similarity to subsp. *tubicula*. Typically such resemblance consists of combinations of strigulose and glandular pubescence or of glandular pubescence and leaves as found in subsp. *strigosus*. Of the collections cited above, intermediacy is shown by *Clark 6710*, *Nelson 4461*, and *Stanford et al. 2472*. Populations in the area of the type locality seem the most distinct from subsp. *tubicula*.

Two plants cultivated from seed had 3 bivalents and 2 rings of 4 chromosomes at meiosis, each thus being heterozygous for 2 translocations. These specimens showed morning anthesis similar to that seen in subsp. *tubicula*. No field collections or observations were made.

Introgression between *C. hartwegii* subsp. *hartwegii* and *C. tubicula* in northern Mexico may have given *C. tubicula* subsp. *strigosus* its distinguishing characteristics. Such hybrid origin may have occurred quite recently since the two forms still occur in close proximity and in similar habitats in the Sierra Madre Oriental. The strigulose pubescence, greater prominence of anthocyanins, and narrow leaves of subsp. *strigosus* in comparison to subsp. *tubicula* all represent points of similarity to the local populations of *C. hartwegii* subsp. *hartwegii*. Of the few collections we have from this area, one set seems to be fully intermediate with *C. hartwegii*, having a floral tube length of 19–21 mm [15 mi SW of Galeana, Nuevo León, *Mueller & Mueller 464* (F, TEX)].

Section II. *Calylophus*.

Calylophus Spach, Hist. Nat. Vég. Phan. 4: 349. 1835. *Oenothera* subgen. *Calylophus* (Spach) Torr. & A. Gray, Fl. N. Amer. 1: 501. 1840.

Meriolix Raf. ex Endl., Gen. Pl. 1190. June 1840; Raf., Amer. Monthly Mag. & Crit. Rev. 4: 192. 1819, nom. nud. Raf., J. Phys. Chim. Hist. Nat. Arts 89: 259. 1819, nom. nud.

Herbaceous to suffrutescent perennials or annuals, 1–8 dm high, glabrous to strigulose or strigulose-canescens. Leaves 1–9 cm long, subentire to spinuose-serrate. Inflorescence dense, with buds usually crowded at the stem apex; buds squarish in cross-section. Flowers opening near sunrise. Floral tube funnelform and somewhat squarish in cross-section distally, tubular in proximal one-third to one-half of length, 2–20 mm long. Sepals with keeled midribs. Petals suborbicular to obcordate. Stamens biseriate, the episealous filaments about twice as long as the epipetalous filaments. Capsule often tardily dehiscent, sometimes slightly recurved.

TYPE SPECIES: *Calylophus serrulatus* (Nutt.) Raven.

5. ***Calylophus berlandieri*** Spach, Ann. Sci. Nat. Bot., sér. 2, 4: 272. 1835.

Herbaceous to suffrutescent perennial or annual arising from a woody caudex; stems one to many, simple to moderately branched, subdecumbent to erect, 1–8 dm high, glabrous to strigulose or strigulose-canescens, especially above. Leaves sessile or indistinctly petiolate, sometimes early deciduous below, spreading to more or less ascending, linear to narrowly lanceolate or oblanceolate, often folded lengthwise, 1–9 cm long, 0.1–0.9 cm wide, usually not much reduced up the stem, the abaxial surface glabrous to strigulose-canescens, especially at the base, the adaxial surface glabrous to sparsely strigulose, the tip acute, the base attenuate, the margin subentire to spinuose-serrate; fascicles of small leaves to 20 mm long often present in nonfloriferous axils; lowest stem leaves narrowly oblanceolate to oblanceolate or even spatulate. Inflorescence more or less compact, with buds usually crowded at the stem apex and one to several flowers fresh at one time, sparsely and minutely strigulose to densely strigulose-canescens; buds squarish in cross-section. Floral tube funnelform and somewhat squarish in cross-section distally, tubular in proximal one-third to one-half of length, 5–20 mm long, 3–14 mm wide at the throat in pressed specimens, subglabrous to strigulose-canescens without, especially along the midribs, within glabrous distally and minutely pubescent to strigulose basally, pale yellow green, sometimes blue black within, rarely fading pinkish. Sepals 4–12 mm long, 2–7 mm wide, with subulate free tips 0–4 mm long, with raised or keeled midribs, subglabrous to strigulose-canescens, pale yellow green, occasionally with red midribs and tips, only rarely fading pinkish. Petals suborbicular to obovate-truncate or obcordate, 6–25 mm long, 7–30 mm wide, occasionally becoming orangish to purplish on wilting, highly ultraviolet-reflective, but with large basal ultraviolet-absorptive spot. Stamens biseriate; episepalous filaments 2–8 mm long, the epipetalous filaments 1–4 mm long; anthers 2–7 mm long; pollen fertility normally 85–100%. Style 9–30 mm long, glabrous above and glabrous to minutely pubescent basally; stigma discoid to squarish, 1–3 mm broad, sometimes blue black, generally exerted to the ends of the anthers or beyond; ovary 5–20(–27) mm long, 0.5–1.5 mm wide, minutely strigulose to strigulose-canescens. Capsule 10–35 mm long, 1–2 mm wide, hard and thick walled, completely and often tardily dehiscent, sometimes slightly recurved; seeds 1–1.8 mm long, sharply angled, truncate at the apex. Self-incompatible. Gametic chromosome number, $n = 7$.

TYPE: UNITED STATES. TEXAS: on shore of Espiritu Santo Bay, probably in present Calhoun Co., March or May 1829, *Jean Louis Berlandier* 539 = 1919 (P, holotype; GH, PH, isotypes). This locality is given on the Gray Herbarium sheet and by Spach (1835b: 338). The date was determined from information given by McKelvey (1955).

Distribution (Fig. 18): Open, moderately dry areas on a variety of well-drained soils, frequently calcareous, in southeastern Colorado, southwestern Kansas, western and central Oklahoma, eastern New Mexico, Texas (except in the northeast), Louisiana, north-central Coahuila, northern Nuevo León, and

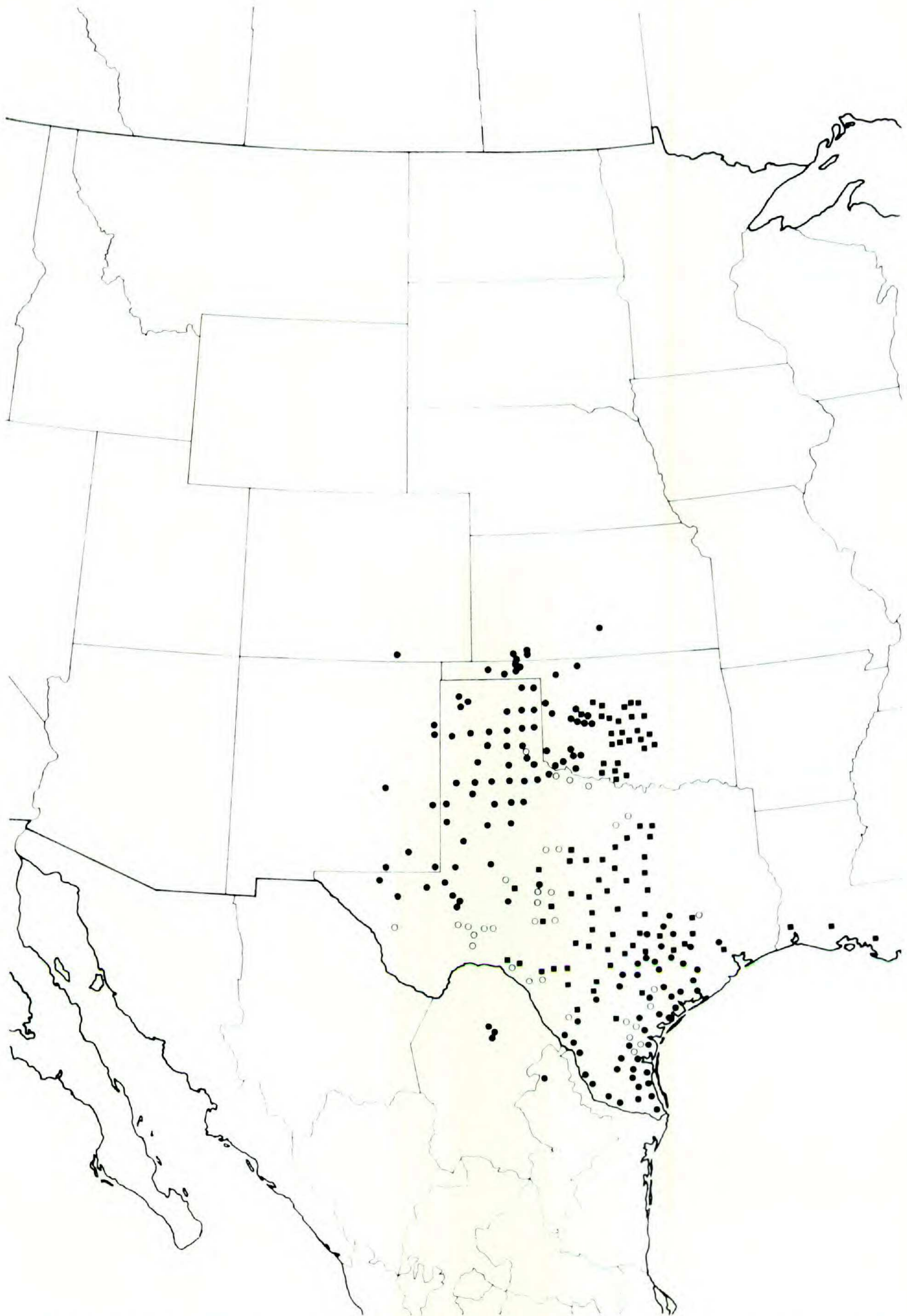


FIGURE 18. Distributions of *Calylophus berlandieri* subsp. *berlandieri* (dots), *C. berlandieri* subsp. *pinifolius* (squares), and intergrades between the two subspecies (open circles).

perhaps northern Tamaulipas. From sea level to ca. 1,200(-1,800) m elevation. Flowering March to September.

An outcrossing species, *Calylophus berlandieri* is characterized by self-incompatibility, large flowers, and the absence of permanent complex structural hybridity. Incompatibility systems of the S-allele type were demonstrated by Linder & Brun (1957) in plants of this species. I tested 24 plants from 6 populations and found all to be self-sterile. The yellow flowers are morning opening, open throated, and have petals with conspicuous contrast patterns in the long-wave ultraviolet region (Fig. 14). A variety of diurnal and matinal insects, including skippers, small butterflies, bees of various families, and beetles, were observed as flower visitors. These groups probably make varying contributions to pollination at different localities, but no highly specific relationship appears to have evolved with any particular type of insect.

Analysis of meiotic pairing in this species demonstrated a high frequency of translocation heterozygosity. Of 68 plants analyzed from 45 populations, 56 or fully 82% were heterozygous for 1 to 5 reciprocal translocations. The most frequent classes of chromosomal types were those with 1 or 2 interchanges, but several plants had as many as 5 translocation heterozygosities. No permanent structural hybridity was proven in this self-incompatible species, but the high frequency of heterozygotes implies that some developmental or selective effect probably reduced the numbers of homozygotes.

As reported by Towner & Raven (1970), Berlandier's type possesses highly fertile pollen, indicative of the pair-forming, outcrossing species in this group. A later examination of the pollen from isotypes of *C. drummondianus* revealed that those plants were only half-fertile. Further study of the specimens and their localities made it obvious that they were complex structural heterozygotes, thus belonging with *C. serrulatus*. This leaves *C. berlandieri* as the earliest available name for the outcrossing species.

The taxonomic separation of *C. berlandieri* from *C. serrulatus* on the basis of differences in cytology and breeding systems rationalized a formerly confusing situation in regard to geographical variation. As previously interpreted, these forms presented a complex pattern of countering trends in variation of floral and vegetative parts. In my treatment, there is less conflict in variation patterns, although the situation is still not simple. The two species exhibit parallel geographic variation, and both display a wide range of statures, leaf dimensions, and flower sizes. The parallelisms are seen primarily in vegetative characters, whereas the floral characters generally differ between the two species.

Calylophus berlandieri is polytypic, with two well-differentiated morphological races. *Calylophus berlandieri* subsp. *pinifolius*, a central Texas subspecies, intergrades with *C. berlandieri* subsp. *berlandieri* in southern and west-central Texas and, to a lesser extent, in the boundary between the Edwards Plateau and the coastal plain.

Populations of this species occasionally occur together with *C. tubicula*, *C. hartwegii*, and *C. lavandulifolius*, but I have seen no evidence of interbreeding. Numerous test crosses performed on those combinations only rarely produced

viable offspring, and these were completely pollen-sterile. Sympatric occurrences with *C. serrulatus* are infrequent, and will be discussed in the section on that species.

KEY TO SUBSPECIES

- a. Stems several to many, subdecumbent to ascending, 1–4 dm tall; leaves 1–4 cm long 5a. subsp. *berlandieri*
 aa. Stems one to several, suberect to erect, 3–8 dm tall; leaves 2.5–9 cm long 5b. subsp. *pinifolius*

5a. *Calylophus berlandieri* Spach subsp. **berlandieri**.

Oenothera berlandieri (Spach) Steud., Nom. Bot., ed. 2. 2: 206. 1841. *Meriolix berlandieri* (Spach) Walp., Repert. Bot. Syst. 2: 79. 1843. *Calylophus drummondianus* Spach subsp. *berlandieri* (Spach) Towner & Raven, Madroño 20: 243. 1970.

Oenothera serrulata Nutt. var. *typica* sensu Munz, Amer. J. Bot. 16: 712. 1929, pro parte. *Calylophus serrulatus* (Nutt.) Raven subsp. *serrulatus* sensu Shinnars, Sida 1: 338. 1964, pro parte. *Oenothera serrulata* subsp. *serrulata* sensu Munz, N. Amer. Fl., ser. 2, 5: 141. 1965, pro parte.

Oenothera serrulata Nutt. var. *pinifolia* Engelm. ex A. Gray sensu Munz, Amer. J. Bot. 16: 715. 1929, pro parte. *O. serrulata* subsp. *pinifolia* (Engelm. ex A. Gray) Munz sensu Munz, N. Amer. Fl., ser. 2, 5: 141. 1965, pro parte.

Oenothera serrulata Nutt. var. *drummondii* Torr. & A. Gray sensu Munz, Amer. J. Bot. 16: 714. 1929, pro parte. *O. serrulata* subsp. *drummondii* (Torr. & A. Gray) Munz sensu Munz, N. Amer. Fl., ser. 2, 5: 142. 1965, pro parte.

Perennial; stems several to many, moderately branched, subdecumbent to ascending, 1–4 dm high. Leaves more or less crowded, linear to narrowly lanceolate or oblanceolate, 1–4 cm long, 0.1–0.6 cm wide, the margin subentire to serrate, and occasionally somewhat undulate; lowest stem leaves frequently oblanceolate to spatulate. Sepals often with only slightly raised midribs, the free tips 0–2 mm long. Inside of floral tube and stigma yellowish, never black. Self-incompatible. Gametic chromosome number, $n = 7$.

Distribution (Fig. 18): Common on grassy prairies, plains, or low hills on sandy, gravelly, and limestone soils in relatively dry areas, frequently with *Prosopis*, *Quercus havardii*, and *Opuntia*, from western Las Animas Co., Colorado, Seward, Meade, and possibly Reno cos., Kansas, south through eastern New Mexico, the Texas Panhandle, and western Oklahoma to Culberson, Ward, and Crane cos., Texas, thence southeast near the Pecos and Rio Grande rivers to the Gulf Coast, becoming widespread on the Coastal Plain north to Milam Co., Texas; also occurring in the Santa Rosa Mts. of northern Coahuila and in northern Nuevo León. From sea level near the Texas coast to ca. 1,200 m (Rita Blanca Lake, Hartley Co., Texas), with one record at ca. 1,800 m elevation (12 mi S of Trinidad, Las Animas Co., Colorado). Flowers March to September.

Representative specimens examined:

UNITED STATES. COLORADO: Las Animas Co.: 12 mi S of Trinidad, *Brenckle 48184* (SMU). KANSAS: Meade Co.: Just S of spillway at Lake Larrabee, Meade Co. State Park, *Bare 24* (KANU). Reno Co.: Hutchinson, *Smyth 40* (US). Seward Co.: 14 mi NE of Liberal, *Stephens 11206* (KANU). NEW MEXICO: De Baca Co.: 35.5 mi S of Ft. Sumner, *Towner 130* (DS). Eddy Co.: 6 mi SW of White's City, *Munz & Gregory 23359* (UC, RSA). 11.4 mi SW of White's City, *Towner 21* (DS). Eddy or Lea Co.: Shinneries E of Carlsbad, *Goodding*

4586 (ARIZ). Lea Co.: S of Jal, *Barneby 14482* (DS). Quay Co.: Porter, *Suggs in 1942* (NMC). Roosevelt or Lea Co.: Between Tatum and Portales, *Goodding in 1937* (ARIZ). OKLAHOMA: Beaver Co.: 15 mi SW of Beaver City, *Stevens 366* (DS, NY, OKL, OKLA, SMU, US). Custer Co.: 1 mi S and 1 W of Weatherford, *Waterfall 1593* (ARIZ, NY). Harmon Co.: 1.1 mi W of Vinson, *Towner 87* (DS). Harper Co.: Supply, *Demaree 12392* (GH, OKL, POM, SMU). Jackson Co.: N bank of Red R., SW of Eldorado, *Towner 138* (DS). 8.8 mi W of Elmer, *Towner 139* (DS). Kiowa Co.: 17.8 mi N of Altus, *Towner 78* (DS). Roger Mills Co.: Antelope Hills, *Goodman 2618* (MO, NY, OKL, POM). Texas Co.: 11 mi E of Hardesty, *Stephens & Brooks 21758* (DS). Tillman Co.: 2.6 mi W of Tipton, *Towner 140* (DS). TEXAS: Aransas Co.: Aransas Bay, *Berlandier 567 = 1957* (GH, MO, POM, RSA). Armstrong Co.: 15 mi S of Claude (Palo Duro Canyon), *Stephens & Brooks 25469* (DS). Bailey Co.: 2 mi S of Muleshoe, *Ferris & Duncan 3397* (DS, MO, NY). Bastrop Co.: Bastrop Park, *Warnock 101* (TEX). Bexar Co.: 20 mi S San Antonio, *Metz 678* (NY, RM). Brooks Co.: 13.4 mi N of Hebbronville, *Towner 57* (DS). 14 mi S of Falfurrias, *Towner 60* (DS). 5 mi N of Falfurrias, *García 49* (OKLA, SMU, TEX). Caldwell Co.: W of Luling, *Crockett 218* (LL). Calhoun Co.: Port O'Connor, *Tharp in 1930* (TEX). 7.5 mi W and 5.6 mi N of Port O'Connor, *Towner 179* (DS). 2.4 mi E of Seadrift, *Towner 180* (DS). Callahan Co.: Ca. 17 mi SE of Abilene, *Henderson 64-52* (DS). Childress Co.: Estelline, *Reverchon 4307* (GH, MO, NY, POM, US). Concho Co.: 2.5 mi W of Eden, *Munz & Gregory 23426* (RSA). Crockett Co.: 25 mi W of Ozona, *McVaugh 8209* (LL, TEX). Dickens Co.: On side of canyon, S of U.S. 82, *Lundell 12979* (LL, TEX, US). Donley Co.: Jericho, *Demaree 12439* (DS, NY, OKL, PH, POM, TEX). Duval Co.: 15 mi E of Hebbronville, *Sandoval & McCart 7982* (OKLA, TEX). Gaines Co.: 3 mi S of Seagraves, *Tharp in 1941* (GH, SMU, TEX). Garza Co.: 2.5 mi E of Post, *Raven & Gregory 19304* (DS). Glasscock Co.: 3 mi E of Garden City, *Munz & Gregory 23422* (RSA, UC). Goliad Co.: Near Goliad, *Williams 9* (F, PH). Harris Co.: Spring, *Gentry 865* (RM). Hartley Co.: 10.4 mi N of Channing, *Roberts 35* (DS). Hemphill Co.: 7 mi ENE of Canadian, *Delso 122* (DS). Hidalgo Co.: 25 mi N of Edinburg, *Clover 811* (NY). Hutchinson Co.: Near Stinnett, *McFarland 13* (OKL, RM). Irion Co.: Barnhart, *Warnock T343* (TEX, US). Jackson Co.: 13.4 mi W Palacios, *Towner 176* (DS). Jim Hogg Co.: 9.7 mi E of Hebbronville, *Towner 56* (DS). Jim Wells Co.: 20 mi N of Premont, *Cabrera 102* (TEX). Kenedy Co.: El Toro I., *Tharp 49123* (in part, possibly a mixture with *C. serrulatus*; F, MO, OKLA, PH, POM, TEX, UC, US). 7.5 mi S of Riviera, *Towner 186* (DS). 17.8 mi N of Raymondville, *Towner 192* (DS). Kleberg Co.: 0.8 mi W of Riviera, *Towner 185* (DS). Kinney Co.: 9 mi W of Brackettville, *McVaugh 7685* (DS, F, SMU, TEX). La Salle Co.: Near Cotulla, *Small & Wherry 11941* (NY). Lee Co.: Giddings, *Hall 209* (F, GH, MO, NY, POM, US). Lipscomb Co.: 23.7 mi N of Canadian, *Rowell 10414* (DS). Live Oak Co.: Mikeska, *Owens & Parks 2407* (MO). Loving Co.: Between Mentone and Wink, *Warnock in 1952* (LL, SMU). Lubbock Co.: N of Lubbock, *Demaree 7528A* (DS, RSA, SMU, TEX). Motley Co.: 5.2 mi WSW of Matador, *Shinners 18668* (OKLA, SMU). Nueces Co.: Bishop, *Eifrig in 1926* (POM). Ochiltree Co.: 11.1 mi SE of Perryton, *Towner 158* (DS). Palo Pinto Co.: 19 mi W of Mineral Wells, *Warren 24* (DS). Pecos Co.: 30 mi W of Sheffield, *Munz 13290* (DS, POM, UC). Potter Co.: 1 mi N of Canadian R. on Highway 287, *Jefferson & Jefferson 2676* (DS, F, MO, NEB, NY, RM, SMU, UC, US, WTU). 11.3 mi N and 2.0 mi W of Amarillo, *Towner 91* (DS). Randall Co.: Palo Duro State Park, *Cory 13036* (LL, SMU). Refugio Co.: 8.9 mi W of Refugio, *McCart 6831* (SMU). San Patricio Co.: Near Mathis, *McKelvey 1726* (GH). Taylor Co.: 3 mi S of Camp Barkeley, *Tolstead 7096, 41983* (MO, NEB, NY, POM, SMU, UC). Terrell Co.: 13 mi S of Sheffield, *Webster 130* (TEX). Tom Green Co.: 7 $\frac{2}{3}$ mi S of Christoval, *Cory 50569* (NY, SMU). Travis Co.: Austin, *Tharp in 1938* (SMU, UC). Uvalde Co.: 6 mi SE of Uvalde, *Munz 13316* (POM). Val Verde Co.: Ca. 1.9 mi from Del Rio, *Traverse 2162* (SMU, TEX). Victoria Co.: Inez, *Palmer 9137* (DS, US). Ward Co.: 3 mi ENE of Monahans, *McVaugh 8186* (DS, GH, LL, TEX). Webb Co.: 7 mi N of Laredo, *Dickey 129* (SMU, TEX). Wheeler Co.: 11.5 mi E of Shamrock, *Rowell 10080* (DS, RSA). Wilbarger Co.: 20 mi N of Vernon, *Towner 77* (DS). Willacy Co.: 1 $\frac{1}{4}$ mi from shore at Port Mansfield, *Webster & Wilbur 3074* (SMU, US). Wilson Co.: 5 mi N of Stockdale, *Munz & Gregory 23443* (RSA, UC). Winkler Co.: 11 mi W of Kermit, *Raven & Gregory 19228* (DS). Wise Co.: 3 mi N of Bridgeport, *Whitehouse 15278a* (SMU). Yoakum Co.: 4.7 mi N of Bronco, *Towner 135* (DS). Zapata Co.: 5 mi SE of San Ygnacio, *Flores & Flores 147* (TEX). Counties not known: From Bejar (San Antonio) to Austin, *Berlandier 479 = 1829* (GH). From Matamoros to Goliad, *Berlandier 1048 = 2478* (GH, MO, PH).

MEXICO. COAHUILA: Santa Rosa Mts., *Marsh 1354* (F, OKLA, SMU, TEX). Múzquiz, *Marsh 110* (F, OKLA, TEX). Hacienda Mariposa, Mepo. of Múzquiz, *Wymd & Mueller 264* (ARIZ, MO, NY, US). Summit of La Cuesta Maleña Mts., *Reveal et al. 2594* (DS). NUEVO LEÓN: Lampazos, *Edwards 356* (F).

This relatively short-leaved and low-statured subspecies occurs over an extensive range on the plains of Texas and adjacent states. It is common in the Texas Panhandle and along the Gulf Coast, and it is also found locally in sandy areas of West Texas. As I have defined it, *Calylophus berlandieri* subsp. *berlandieri* incorporates elements from each of the three subspecies of "*Oenothera serrulata*" recognized by Munz (1965: 141-142).

For instance, the extremely narrow-leaved plants formerly known as *Oenothera serrulata* subsp. *pinifolia* are clearly variants which can actually be found along with broader-leaved plants in populations of either subspecies of *C. berlandieri*. My treatment of these forms is similar to that of Shinnars (1964), who did not recognize subsp. *pinifolia*, viewing it as merely the extreme in a wide range of variation, the latter due to "spontaneous mutation." The narrow-leaved plants are most frequently found in areas of highly calcareous soil, including gypsum, and they occur in the more arid portions of the range of *C. berlandieri*. Thus their presence may well be due not to "spontaneous mutations," but to edaphic selection factors.

In the past, narrow-leaved individuals of *C. berlandieri* subsp. *berlandieri* were often assigned to *Oenothera serrulata* var. *pinifolia*. Examples are the following: 5 mi N of Stockdale, Wilson Co., Texas, *Munz & Gregory 23443* (UC, RSA). 2 mi S of Muleshoe, Bailey Co., Texas, *Ferris & Duncan 3397* (DS, MO, NY). Narrow-leaved individuals are slightly more frequent in *C. berlandieri* subsp. *pinifolius*, although they are not representative of that taxon as a whole.

The distribution of *C. berlandieri* subsp. *berlandieri* is divided into a Coastal Plains section and a Central Plains section. These two series of populations are connected only tenuously, this through a narrow zone along the Rio Grande southwest of the Edwards Plateau. The coastal region is less severe in climate than is the central region, but both areas are semiarid. Considering the breadth of these separate ranges, their distinctness, and their climatic differences, one might expect the two series of populations to have diverged morphologically. However, this does not appear to have been the case, as they show completely overlapping ranges of variation in all characters which I have examined.

In spite of the morphological similarity of the two series, meiotic pairing in hybrids suggests that considerable cytological divergence may have taken place. Nine hybrids between progeny of *Rowell 10414* (Lipscomb Co., Texas) and progeny of *Bohart & Thorp 650928-1* (Victoria Co., Texas) showed I₂/KI pollen stainability of approximately 40%. Meiotic determinations of 2 of the hybrids showed chains of 14 chromosomes, indicating the presence of at least 6 reciprocal translocation differences between the parents. Similar data were obtained from crosses of Rowell's collection with *Towner 185* (Kleberg Co., Texas).

The frequency of translocation heterozygosity in natural populations of *Calylophus berlandieri* subsp. *berlandieri* was found to be extremely high. Of 38

plants examined, including some grown from field-collected seed, only 6 formed 7 bivalents at meiotic metaphase. The remaining 84% showed multivalent formation in various degrees, indicating structural heterozygosity. The average number of translocations per plant was 2.0.

Flower visitation was observed at one site in Potter Co., Texas (*Towner 91*). Anthesis occurred shortly before sunrise, at which time several hawkmoths (*Hyles lineata*) visited flowers for nectar. At sunrise and afterwards, skippers, small butterflies, and bees of small to medium size, e.g., *Evyllaenus* and *Agapostemon*, collected nectar and pollen from the flowers. Pollination was perhaps most effective with the anthophorid bees (*Melissodes* and *Anthophora*), which were few in number, however. Oligolectic halictids probably made some contribution, since they were common and because their appearance coincided closely with anthesis times.

Intergradation occurs between *C. berlandieri* subsp. *berlandieri* and *pinifolius* in several areas. Along the eastern escarpment of the Edwards Plateau, few natural intermediates are found, apparently because the respective habitats of the two forms are separated by a relatively sharp geographical discontinuity. On the southern and western sides of the Plateau, intermediate forms are much more frequent. There the geographical changes are more gradual, and broad zones of hybridization are evident. On the western side of the range of *C. berlandieri* subsp. *pinifolius*, numerous plants intermediate in stature and leaf length are found: 25 mi W of Ozona, Crockett Co., Texas, *McVaugh 8209* (LL, TEX). 3 mi S of Camp Barkeley, Taylor Co., Texas, *Tolstead 7096, 41983* (MO, NEB, NY, PO, SMU, UC). 3 mi E of Garden City, Glasscock Co., Texas, *Munz & Gregory 23422* (RSA, UC). Similarly, collections intermediate between *C. berlandieri* subsp. *pinifolius* and the Rio Grande Valley populations of subsp. *berlandieri* are relatively frequent. Several examples are as follows: Ca. 1.9 mi from Del Rio, Val Verde Co., Texas, *Traverse 2162* (SMU, TEX). 9 mi W of Brackettville, Kinney Co., Texas, *McVaugh 7685* (DS, F, SMU, TEX). 6 mi SE of Uvalde, Uvalde Co., Texas, *Munz 13316* (POM).

Over much of its distribution, *C. berlandieri* subsp. *berlandieri* occurs with or near populations of species of sect. *Salpingia*. In most cases of sympatry a few plants of one form are found scattered in or near a colony of the other, and only rarely are both forms common at any locality. The taxa I observed growing together with *C. berlandieri* subsp. *berlandieri* were *C. hartwegii* subsp. *filifolius* in De Baca Co., New Mexico and *C. hartwegii* subsp. *pubescens* in the Texas Panhandle. Also occurring with *C. berlandieri* subsp. *berlandieri* in the Panhandle and in western Oklahoma, but more distinct ecologically, are *C. hartwegii* subsp. *fendleri* and *C. lavandulifolius*. In West Texas there is some likelihood of contact between *C. tubicula* and *C. berlandieri* subsp. *berlandieri*, although their edaphic restrictions seem to reduce this possibility severely. Lastly, local sympatry may also occur with *C. hartwegii* subsp. *maccartii* in the lower Rio Grande Valley, since the edaphic and geographical ranges of the two forms overlap there.

5b. *Calylophus berlandieri* Spach subsp. **pinifolius** (Engelm. ex A. Gray)
Towner, comb. nov.—FIG. 5.

- Oenothera serrulata* Nutt. var. *pinifolia* Engelm. ex A. Gray, Boston J. Nat. Hist. 6: 189. 1850; Munz, Amer. J. Bot. 16: 715. 1929. *Meriolix serrulata* (Nutt.) Raf. (var.) *pinifolia* (Engelm. ex A. Gray) Small, Bull. Torrey Bot. Club 23: 187. 1896. *Oenothera serrulata* subsp. *pinifolia* (Engelm. ex A. Gray) Munz, N. Amer. Fl., ser. 2, 5: 141. 1965.
- Oenothera capillifolia* Scheele, Linnaea 21: 576. 1848. *Meriolix capillifolia* (Scheele) Small, Fl. S.E. U.S. 846, 1335. 1903. TYPE: United States, Texas, Comal Co., New Braunfels, April (1846?), *Ferdinand Roemer* (not located).
- Meriolix hillii* Small, Fl. S.E. U.S. 846, 1335. 1903. TYPE: United States, Texas, Edwards Co., Frio Water Hole, 30 June 1895, *R. T. Hill* (NY).
- Meriolix melanoglottis* Rydb. ex Small, Fl. S.E. U.S. 846, 1335. 1903. *Oenothera serrulata* Nutt. var. *maculata* H. Lév., Monogr. Onoth. 336, 339. 1908 (lectotype: *Heller 1600*, MO). TYPE: United States, Texas, Kerr Co., Kerrville, 19–25 April 1894, *A. A. Heller 1600* (NY, holotype; ARIZ, MO, NEB, NY, PH, POM, RM, SMU, UC, US, isotypes).
- Oenothera serrulata* Nutt. var. *drummondii* Torr. & A. Gray sensu Munz, Amer. J. Bot. 16: 714. 1929, pro parte. *O. serrulata* subsp. *drummondii* (Torr. & A. Gray) Munz sensu Munz, N. Amer. Fl., ser. 2, 5: 142. 1965, pro parte.
- Oenothera serrulata* Nutt. var. *drummondii* Torr. & A. Gray f. *flava* Munz sensu Munz, Amer. J. Bot. 16: 714. 1929, for the most part, excluding the type.
- Calylophus serrulatus* (Nutt.) Raven var. *spinulosus* (Torr. & A. Gray) Shinnery sensu Shinnery, Sida 1: 339. 1964, pro parte.
- Calylophus drummondianus* Spach subsp. *drummondianus* sensu Towner in Correll & Johnston, Man. Vasc. Pl. Texas 1123. 1970, all, except for the type.

Annual to short-lived perennial; stems one to several, simple or sparsely branched, suberect to erect, 3–8 dm high. Leaves well spaced, linear to narrowly oblanceolate or narrowly lanceolate, 2.5–9 cm long, 0.2–0.9 cm wide, the margin remotely serrulate to spinuose-serrate; lowest stem leaves narrowly oblanceolate. Sepals with conspicuously keeled midribs, with free tips 0.5–4 mm long. Stigma and inside of floral tube frequently deep blue black in certain populations. Self-incompatible. Gametic chromosome number, $n = 7$.

TYPE: UNITED STATES. TEXAS: Comal Co., rocky prairies, New Braunfels, April 1846, *Ferdinand Lindheimer 37 = 394* (GH, holotype; DS, MO, NY, PH, RSA, US, isotypes).

Distribution (Fig. 18): Common on prairies and in open places in oak savanna, on rocky, clay, or sandy soils, often calcareous, from Blaine and Lincoln cos., Oklahoma, south through a narrow portion of north-central Texas to central Texas, where it is widely distributed, especially on the Edwards Plateau; also occurs locally in western and southern Louisiana. Elevational distribution from near sea level (Sulfur, Calcasieu Parish, Louisiana) to ca. 900 m (Sonora, Sutton Co., Texas). Flowers mostly from March to June.

Representative specimens examined:

UNITED STATES. MISSOURI: Jackson Co.: Sheffield (introduced), *Bush 328* (F, GH). OKLAHOMA: Blaine Co.: 3 mi W of Greenfield, *Hopkins & van Valkenburgh 4131* (OKL). Caddo Co.: Rim of Devil's Canyon, *Hopkins et al. 309* (DS, F, MO, OKL, OKLA, RM, SMU, UC, WTU). Canadian Co.: 2 mi W of El Reno, *Munz & Gregory 23505* (RSA, UC, WTU). Cleveland Co.: Norman, *Demaree 12473* (MO, NY, OKL, POM, RM, SMU). Cotton Co.: 6.9 mi E of Walters, *Towner 141* (DS). 9 mi W of Comanche, *Towner 142* (DS). Custer Co.: Ca. 1.5 mi W of Custer, *Towner 154* (DS). Lincoln Co.: 3.2 mi S of Perkins, *Towner 149B* (DS). Logan Co.: 15 mi W of Guthrie, *Raven & Gregory 19462* (DS). 5.4 mi W of Guthrie, *Towner 151* (DS). McClain Co.: Blanchard (Johnson's Pasture), *Demaree 13094* (MO, NY,

OKL, PH, POM, TEX, UC, US). Oklahoma Co.: 6 mi W and 6 N of Oklahoma City, *Waterfall* 1423 (OKL, POM). Seminole Co.: SE of Konawa, *Robbins* 2458 (OKL, UC). Stephens Co.: S of Comanche, *Waterfall* 3679 (NY, OKL). TEXAS: Austin Co.: Bellville, *Fisher* 3846 (F). Bastrop Co.: S of Bastrop, *Lundell & Lundell* 10355 (ARIZ, LL, POM, US). Bell Co.: 5 mi S of Temple, *Wolff* 4037 (F). Bexar Co.: San Antonio, *Clemens & Clemens* 686 (NY, PH, POM, RM). Blanco Co.: 2 mi S of Blanco, *Tharp et al.* 17T195 (RM, SMU). 5.5 mi N of Johnson City, *Towner* 68 (DS). 32.7 mi NW of San Marcos, *Towner* 66 (DS). Brown Co.: 8.2 mi S of Brownwood, *Towner* 72 (DS). Brownwood, *Ewing* 26 (LL, SMU, TEX). Burnet Co.: Burnet, *Fisher* 40065 (ARIZ, NEB, TEX). Coke Co.: 2 mi E of Robert Lee, *Shinners* 31773 (SMU). Coleman Co.: 14.3 mi N of Coleman, *Towner* 74 (DS). Comal Co.: New Braunfels, *Lindheimer* 809 (ARIZ, DS, F, GH, MO, NMC, NY, OKL, PH, TEX, UC, US). 20.9 mi NW of San Marcos, *Towner* 64 (DS). Comanche Co.: Round Top Mt., *Eggert in 1900* (MO). Coryell Co.: 13 mi E of Gatesville, *Jackson* 4 (LL, SMU, TEX). Crockett Co.: 30 mi N of Juno, *Warnock* 15289 (LL, TEX). Dallas Co.: White Rock Lake, *Lundell & Lundell* 8531 (DS, GH, LL, POM, SMU). Dimmit Co.: Carrizo Springs, *Palmer* 33732 (MO). Ellis Co.: 1½ mi N of Midlothian, *Cory* 53327 (DS, KANU, RM, SMU, UC). Erath Co.: 3.5 mi W of Stephenville, *Gould* 5644 (RSA, SMU, UC). Fayette Co.: La Grange, *Hanisch in 1935* (TEX). Frio Co.: 6 mi NE of Pearsall, *Lundell* 13628 (LL, TEX). Gillespie Co.: Bear Mt., *Correll & Correll* 12763 (LL, SMU). Hamilton Co.: Hamilton, *Tharp in 1941* (GH). Harris Co.: Houston, *Fisher* 3481 (F). Hays Co.: 5 mi W of San Marcos, *Gregory* 419 (DS, RSA, US). 5.1 mi NW of San Marcos, *Towner* 62 (DS). 7.5 mi NW of San Marcos, *Towner* 63 (DS). Hill Co.: 8.5 mi NE of Hillsboro, *Shinners* 12494 (SMU). Hood Co.: Grandbury, "Naples School" 7174 (US). Irion Co.: 30 mi N of Barnhart, *Raven & Gregory* 19210 (DS). Karnes Co.: 3 mi SE of Karnes City, *Johnson* 857 (RSA, TEX). Kendall Co.: 19 mi S of Fredericksburg, *Munz & Gregory* 23438 (RSA, WTU). Kerr Co.: 4 mi SW of Kerrville, *Cory* 51763 (DS, SMU). Kimble Co.: No locality, *Tharp* 43-738 (TEX, UC). Kinney Co.: Ca. 30 mi SE of Brackettville, *Strother* 240 (DS, SMU). Lampasas Co.: 1 mi S of Lampasas, *Whitehouse* 15384 (SMU). Llano Co.: No locality, *Lundell & Lundell* 9050 (DS, GH, LL, POM, SMU). 1.7 mi N of Llano, *Towner* 69 (DS). Medina Co.: Hondo, *Pilsbry in 1903* (PH). Menard Co.: 10.3 mi N of Menard, *Raven & Gregory* 19273 (DS). McClennan Co.: Between Waco and McGregor, *York* 46074 (TEX, UC). McCulloch Co.: 9 mi SE Brady, *Munz & Gregory* 23431 (RSA, UC, WTU). McMullen Co.: No locality, *Schultz* 64 (US). Mills Co.: Goldthwaite, *Ferguson* 4-21 (MO, PH, TEX, UC). San Saba Co.: 4 mi W of Pontotoc, *Jones* 24 (LL, SMU). Sutton Co.: Sonora, *Tharp in 1931* (TEX). Tarrant Co.: Lake Como, *Ruth* 30 (F). Travis Co.: 9 mi W of Oak Hill, *Lundell & Lundell* 8898 (DS, GH, LL, NY, POM, RM, SMU, UC). Uvalde Co.: 20 mi N of Uvalde, *Graves* 9 (RM, RSA). Val Verde Co.: Devil's R. N of Del Rio, *Pilsbry in 1903* (PH). Washington Co.: No locality, *Brackett in 1938* (GH). Williamson Co.: No locality, *York* 46193 (TEX). LOUISIANA: Acadia Parish: Prairies near Crowley, *Small & Wherry* 11741 (NY). Calcasieu Parish: Sulphur, *Palmer* 7719 (MO). St. Mary Parish: Near Berwick, *Small & Wherry in 1925* (NY).

As with *Calylophus berlandieri* subsp. *berlandieri*, subsp. *pinifolius* incorporates portions of several of the taxa recognized by earlier authors. It corresponds rather closely with *Oenothera serrulata* subsp. *drummondii* except for the inclusion of narrow-leaved individuals and exclusion of complex heterozygotes. As mentioned earlier, the types seen of *C. drummondianus* were erroneously assigned to the outcrossing species in a preliminary report (Towner & Raven, 1970). The types actually belong with the complex structural heterozygote *C. serrulatus*, and the name is reduced to synonymy. The collection used as the basis for *Oenothera serrulata* var. *drummondii* f. *flava* was also found to belong with *C. serrulatus*, having the small flowers and half-sterile pollen indicative of complex structural heterozygosity.

Calylophus berlandieri subsp. *pinifolius* is distributed primarily from central Texas to central Oklahoma, inhabiting more mesic areas than does subsp. *berlandieri*. Most typically it is found in calcareous, rocky soil in oak savanna. Colo-

nies occur in open or disturbed areas in that habitat and in prairies. This subspecies is the only member of sect. *Calylophus* occurring on the Edwards Plateau in Texas.

Earlier reference was made to the narrow-leaved variants occurring in the two subspecies of *C. berlandieri*. The presence of these forms in both taxa prevents the use of leaf proportion as a diagnostic or key character. However, *C. berlandieri* subsp. *pinifolius* is distinctly longer leaved than subsp. *berlandieri*, and the use of this character together with differences in stature permits an easy diagnosis of most individuals. Subspecies *pinifolius* generally has a slender taproot and is difficult to maintain for more than a year in the greenhouse, leading to the inference that it is probably a short-lived perennial or annual in the field. This contrasts with subsp. *berlandieri*, which is distinctly perennial over most of its range.

Some representatives of this subspecies possess purplish black stigmas and/or inner surface of the floral tubes. This extremely interesting character is present as a polymorphism in many populations, but is restricted to those in south-central Texas. The dark-pigmented forms are especially frequent in Bexar, Blanco, Comal, Gillespie, Hays, Kendall, Kerr, and Travis cos. Some examples of the variants include the following collections: Type specimen of *Meriolix melanoglottis* Rydb. ex Small. Type specimen of *Meriolix hillii* Small. 19 mi S of Fredericksburg, Kendall Co., Texas, *Munz & Gregory 23438* (RSA, WTU). 7.5 mi NW of San Marcos, Hays Co., Texas, *Towner 63* (DS; most plants with black stigma, some with black hypanthium). 5.5 mi N of Johnson City, Blanco Co., Texas, *Towner 68* (DS; plants with black stigma only). U.S. 87 near NW city limits of San Antonio, Bexar Co., Texas, *Klein 1671-1674* (DS). New Braunfels, Comal Co., Texas, *Lindheimer 809* (ARIZ, DS, F, GH, MO, NMC, NY, OKL, PH, TEX, UC, US). 4 mi SW of Kerrville, Kerr Co., Texas, *Cory 51763* (DS, SMU).

Plants from populations of *C. berlandieri* subsp. *pinifolius* from Oklahoma differ modally from those in Texas in having shallower leaf serrations and more strigose pubescence on the upper stems. This is especially apparent in the northernmost populations, e.g., those in Logan, Oklahoma, McClain, and Cleveland cos. In regard to stature, leaf dimensions, and most other characters, these plants are identical to individuals from Texas populations of subsp. *pinifolius*. Some of the largest-flowered members of the species occur in these Oklahoma populations. Examples of plants from this area are as follows: 5.4 mi W of Guthrie, Logan Co., Oklahoma, *Towner 151* (DS). Norman, Cleveland Co., Oklahoma, *Demaree 12767* (OKL, POM, SMU). Blanchard, McClain Co., Oklahoma, *Demaree 13094* (MO, NY, OKL, PH, POM, TEX, UC, US).

As in *C. berlandieri* subsp. *berlandieri*, this subspecies has a great deal of translocation heterozygosity. Of the 30 plants which have been examined, 24 or 80% had ring or chain multivalents at meiotic metaphase I. Of these plants, those having 1 or 2 heterozygosities were the most frequent types. The average number per plant was 1.6.

Floral behavior has been observed in Brown Co., Texas (*Towner 72*) and in the greenhouse at Stanford, California. Anthesis took place shortly after sun-

rise. Insect visitors to flowers observed by me, and by P. H. Raven and D. P. Gregory in Hays and Kyle cos., Texas (personal communication), included small butterflies, flies, skippers [*Atalopedes campestris* (Boisduval)], a variety of beetles, especially cantharids and *Acmaeodera* (Buprestidae), numerous small bees (*Agapostemon*, *Augochlorella*, *Dialictus*, *Evylaeus*, and *Halictus*), and a few large and medium-sized bees (*Apis*, *Bombus*, *Megachile*, *Xylocopa*, anthophorids). It seems likely that a broad spectrum of insects serves as pollen vectors. Skippers, medium-sized bees, and beetles, judged by their abundance, size, and contact with the anthers and stigma, may be the primary pollinating agents for most populations. The black floral tubes and stigmas, which occur together with large ultraviolet patterns, may complement those patterns in facilitating the orientation of visiting insects. This would be especially important for any species of insect which lacked the tricolor vision of bees and could not discriminate in the ultraviolet region of the spectrum.

With no evidence of hybridization, *C. berlandieri* subsp. *pinifolius* occurs together with *C. hartwegii* subsp. *pubescens* in much of its range in central and west-central Texas. No other member of sect. *Salpingia* overlaps significantly in distribution with subsp. *pinifolius*. Minor geographic sympatry exists in southern Texas with *C. hartwegii* subsp. *maccartii* and in western Texas with *C. tubicula* subsp. *tubicula* and *C. hartwegii* subsp. *filifolius*. In these cases, local sympatry is quite infrequent or absent, probably as a result of habitat segregation.

6. *Calylophus serrulatus* (Nutt.) Raven, Brittonia 16: 286. 1964.—FIG. 6.

- Oenothera serrulata* Nutt., Gen. N. Amer. Pl. 1: 246. 1818. *Meriolix serrulata* (Nutt.) Raf., Amer. Monthly Mag. & Crit. Rev. 4: 192. 1819. *Calylophus nuttallii* Spach, Hist. Nat. Vég. Phan. 4: 350. 1835. *Oenothera serrulata* var. *nuttallii* (Spach) Torr. & A. Gray, Fl. N. Amer. 1: 501. 1840. *Meriolix serrulata* var. *nuttallii* (Spach) Walp., Repert. Bot. Syst. 2: 79. 1843. *Oenothera serrulata* var. *typica* Munz, Amer. J. Bot. 16: 712. 1929. *Calylophus serrulatus* (Nutt.) Raven var. *serrulatus*; Shinnery, Sida 1: 338. 1964. *Oenothera serrulata* subsp. *serrulata*; Munz, N. Amer. Fl., ser. 2, 5: 141. 1965.
- Oenothera leucocarpa* Comien ex Lehm. in Hooker, Fl. Bor. Amer. 1: 210. 1833. *O. serrulata* Nutt. var. *douglasii* Torr. & A. Gray, Fl. N. Amer. 1: 502. 1840. *Meriolix serrulata* (Nutt.) Raf. var. *douglassii* (Torr. & A. Gray) Walp., Repert. Bot. Syst. 2: 79. 1843. TYPE: Canada, Saskatchewan, common on limestone rocks on Red and Assiniboine rivers, August 1827, David Douglas (K, lectotype).
- Calylophus drummondiana* Spach, Ann. Sci. Nat. Bot., sér. 2, 4: 272. 1835. *Oenothera serrulata* Nutt. var. *drummondii* Torr. & A. Gray, Fl. N. Amer. 1: 502. 1840. *O. spachiana* Steud., Nom. Bot., ed. 2, 2: 207. 1841. *Meriolix serrulata* (Nutt.) Raf. var. *drummondii* (Torr. & A. Gray) Walp., Repert. Bot. Syst. 2: 79. 1843. *M. drummondiana* (Spach) Small, Fl. S.E. U.S. 846, 1335. 1903. *Oenothera serrulata* subsp. *drummondii* (Torr. & A. Gray) Munz, N. Amer. Fl., ser. 2, 5: 142. 1965, pro parte. *Calylophus drummondianus* subsp. *drummondianus*; Towner in Correll & Johnston, Man. Vasc. Pl. Texas 1123. 1970. TYPE: United States, Texas, along the Rio Brazos on the Texas coastal plain, probably between Brazos Co. and the coast, 1833, Thomas Drummond (P, holotype; GH, NY, isotypes, but not Drummond III. 79 at PH).
- Oenothera serrulata* Nutt. var. *spinulosa* Torr. & A. Gray, Fl. N. Amer. 1: 502. 1840. *Meriolix serrulata* (Nutt.) Raf. var. *spinulosa* (Torr. & A. Gray) Walp., Repert. Bot. Syst. 2: 79. 1843. *M. spinulosa* (Torr. & A. Gray) Heller, Contr. Herb. Frankl. & Marsh. 1: 70. 1895. *Calylophus serrulatus* (Nutt.) Raven var. *spinulosus* (Torr. & A. Gray) Shinnery, Sida 1: 339. 1964. TYPE: United States, Oklahoma, vicinity of the Red R., probably near present-day Choctaw Co., May–June 1819, Thomas Nuttall, Torrey Herb. [NY, lectotype; PH, NY, isolectotypes, but not “Red River, Nuttall,” (GH), or “Arkansas,” (PH)]. Some of Nuttall’s Red River and Arkansas collections, such as the GH specimen cited, are actually

- Calylophus berlandieri*. The type sheet has the Leavenworth specimen cited by Torrey and Gray mounted next to the Red River type of Nuttall.
- Meriolix intermedia* Rydb. ex Small, Fl. S.E. U.S. 846, 1335. 1903. TYPE: United States, Missouri, Atchison Co., Watson, 7 June 1894, *B. F. Bush* 321 (NY, holotype; MO, OKL, isotypes).
- Oenothera serrulata* Nutt. var. *integrifolia* H. Lév., Monogr. Onoth. 337, 339. 1908. TYPE: United States, probably from southeastern Colorado, 1945, third expedition of John C. Fremont, no. 47 (MO); Munz, Amer. J. Bot. 16: 713. 1929.
- Oenothera serrulata* Nutt. var. *drummondii* Torr. & A. Gray f. *flava* Munz, Amer. J. Bot. 16: 714. 1929. TYPE: United States, Texas, Walker Co., Huntsville, *B. C. Tharp* 866 (POM-32801; other collections cited in the protologue are *C. berlandieri* subsp. *pinifolius*).
- Meriolix oblanceolata* Rydb., Brittonia 1: 93. 1931. TYPE: United States, Kansas, Comanche Co., along road 2 mi W of Coldwater, 8 July 1929, *P. A. Rydberg* & *R. Imler* 737 (NY, holotype; KANU, NEB, NY, isotypes).
- Calylophus serrulatus* (Nutt.) Raven var. *arizonicus* Shimmers, Sida 1: 338. 1964. TYPE: United States, Arizona, Navajo Co., dry sandy riverbank 4 mi upstream from White River, 25 June 1951, *S. J. Preece, Jr.* & *B. L. Turner* 2692 (SMU).
- Calylophus australis* Towner & Raven, Madroño 20: 243. 1970. TYPE: United States, Texas, Cameron Co., Texas route 4, 2.8 mi W of end of road at Boca Chica, 29 May 1969, *Towner* 187 (DS-612434, holotype; RSA, TEX, US, isotypes).

Similar to *Calylophus berlandieri*. Herbaceous to suffrutescent perennial from a woody caudex; stems few to many, 1–6 dm high. Floral tube 2–12(–16) mm long, 3–12 mm wide, never blue black within. Sepals 1.5–9 mm long, 2–6 mm wide. Petals 5–12(–20) mm long, 5–15(–20) mm wide. Episepalous filaments 1–5(–7) mm long, the epipetalous filaments 0.5–3 mm long; anthers 1.5–4(–7) mm long; pollen grains 30–80% aborted. Style 2–15(–20) mm long; stigma 1–2 mm broad, not exerted beyond the anthers, and often in contact with the anthers at the apex of the floral tube, never blue black; ovary 4–13 mm long. Self-compatible and highly autogamous. Gametic chromosome number, $n = 7$, with a ring of 14 chromosomes or a ring of 12 plus a bivalent at meiotic metaphase I.

TYPE: UNITED STATES. Plains along the Missouri River, probably just north of the Platte River in eastern Nebraska, April or May 1811, *Thomas Nuttall* (PH). From Bradbury's account of the expedition (McKelvey, 1955: 115–118) and because of the immature appearance of the type, these dates seem more likely than June, the date of flowering given in the original description.

Distribution (Fig. 19): Common on plains, in grassy open areas in woods, or, rarely, in mountains, usually on sandy or rocky soils, from southern Alberta, southern Saskatchewan, and southern Manitoba to eastern New Mexico, the Texas Panhandle, and the Gulf Coast of Texas, including eastern Montana, eastern Wyoming, eastern Colorado, North Dakota, South Dakota, Nebraska, Kansas, western and central Oklahoma, western and southern Minnesota, Iowa, northwestern Missouri, and with outlying populations in southeastern Wisconsin, northwestern peninsular Michigan, east-central Arizona, and west-central Chihuahua, Mexico. Elevational distribution from sea level along the Texas coast to 2,100 m (18 mi N of Rubio, Chihuahua). Flowers March to August.

Representative specimens examined:

CANADA. ALBERTA: Near Peigan, *Moss* 871 (DAO, NY). SASKATCHEWAN: Katepwa, *Russell* 54519 (DAO). Pilot Butte, *Hart in* 1939 (DAO, UC). 13 mi W of Saskatoon, *Shumovich* 38 (CAN, DAO, RM). Moose Jaw, *Turner* 48 (GH, NY, POM, RSA). MANITOBA:

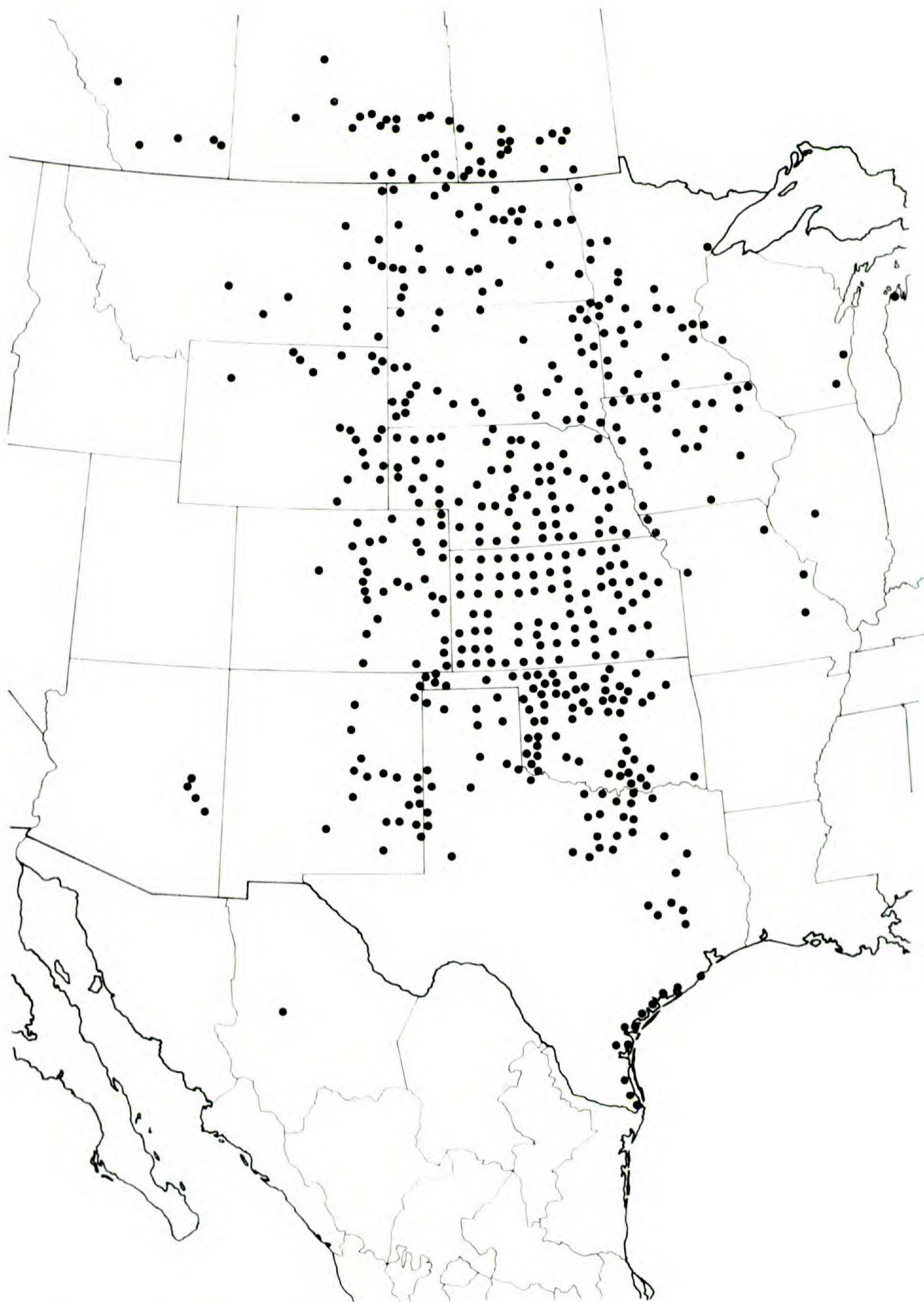


FIGURE 19. Distribution of *Calylophus serrulatus*.

Brandon, *Fowler in 1887* (DAO, MO, NY, US). Horton, *Love & Love 6081* (DAO, GH). Melita, *Scoggan 9794* (CAN, GH). Mouth of the Qu'Appelle R., *Macoun & Herriot 72,377* (F, GH, NY).

UNITED STATES. MONTANA: Billings Co.: 1.5 mi S of Medora, *Stephens & Brooks 13486*

(KANU). Powder River Co.: 15 mi NW of Boradus, *Booth 2517* (KANU, WTU). Prairie Co.: 32 mi NW of Terry, *Stephens & Brooks 23691* (DS). Sheridan Co.: Westby, *Larsen 213* (GH, NY). Wheatland Co.: 12 mi S of Harlowton, *Hitchcock 2429* (MO, POM, RSA). NORTH DAKOTA: Barnes Co.: Valley City, *Stevens in 1934* (F, RM, UC). Divide Co.: Alkabo, *Larsen 88* (GH, MO, PH). Dunn Co.: 10 mi NW of Killdeer, *Stephens & Brooks 12734* (DS, KANU). Golden Valley Co.: 1 mi E and 1 S of Sentinel Butte, *Stephens & Brooks 23428* (DS). Slope Co.: 7 mi S of Amidon, *Cutler 2615* (DS, MO, NY). Ward Co.: 9 mi NW of Minot, *Stephens & Brooks 12897* (DS, KANU). SOUTH DAKOTA: Custer Co.: 14 mi S of Pringle, *Stephens & Brooks 13798* (DS, KANU). Harding Co.: 6 mi N, 11 W, and 2 N of Ludlow, *Stephens & Brooks 13657* (DS, KANU). Lawrence Co.: 0.8 mi N of Spearfish, *Mosquin & Mulligan 5160* (DS). Meade Co.: Near Fort Meade, *Forwood 130* (CAN, US). Pennington Co.: Rapid City, *Rydberg 708* (F, GH, NEB, NY, US). Perkins Co.: 10 mi E and 1 S of Bison, *Stephens 7999* (KANU, SMU). MINNESOTA: Chippewa Co.: Montevideo, *Moyer in 1908* (NY, UC). Dakota Co.: 5.5 mi W of Hastings, *Moore 15797* (DAO, GH). Faribault Co.: Elmore, *Pammel 596* (GH, MO, RM, US). Nicollet Co.: No locality, *Aiton in 1891* (F, NY, POM, US). Ottertail Co.: Perham, *Chandonnet in 1910, 1911* (GH, RM). Yellow Medicine Co.: S side of Granite Falls, *Moore 13071* (SMU, UC). WISCONSIN: Pepin Co. (?): Lake Pepin, *Hale 1861* (F, MO). WYOMING: Converse Co.: 15 mi N of Douglas, *Stephens & Brooks 23965* (DS). Crook Co.: 5 mi NE of Hulett, *Porter & Porter 9564* (CAN, DS, RM, RSA, UC, WTU). Goshen Co.: 12 mi W of Lagrange, *Stephens & Brooks 22947* (DS). Niobrara Co.: 10 mi N of Lusk, *Mosquin & Mulligan 5142* (DS). Platte Co.: Guernsey, *Nelson 8268* (DS, F, GH, MO, NEB, NY, POM, RM, RSA, UC, US). 3 mi W of Guernsey, *Porter 4903* (COLO, DS, GH, MO, PH, RM, RSA, SMU, TEX, WTU). NEBRASKA: Adams Co.: 20 mi W of Hastings, *Mathias 308* (MO, POM). Chase Co.: 6 mi N of Imperial, *Stephens & Brooks 11490* (KANU). Cherry Co.: Vicinity of Hackberry Lake, *Dworak in 1912* (NEB). Dawes Co.: Chadron State Park, *Porter & Porter 8807* (DS, RM, WTU). Garden Co.: 2 mi S of Lewellen, *Stephens & Brooks 11557* (KANU). Greeley Co.: 9 mi N of Greeley, *McGregor 19344* (KANU). Hayes Co.: 14 mi W of Hayes Center, *Stephens & Brooks 13958* (DS, KANU). Holt Co.: 12.5 mi S of Atkinson, *Stephens 15579* (KANU). Kearney Co.: Minden, *Hapeman in 1930* (OKLA, TEX). Lincoln Co.: North Platte, *Jones in 1925* (DS, POM). Morrill Co.: 27 mi N of Broadwater, *Stephens & Brooks 13888* (DS, KANU). Saunders Co.: 4 mi S of Valparaiso, *Croat 2126, 2127* (KANU, MO). Sheridan Co.: 13.5 mi S of Hay Springs, *Stephens & Brooks 13839* (DS, KANU). Webster Co.: S of Blue Hill, *Tolstead 411245* (NEB, UC). IOWA: Emmet Co.: No locality, *Cratty, s.n.* (DS, F, NY, PO, UC). Fremont Co.: Hamburg, *Bush 10313* (GH, MO, PH, POM). Lyon Co.: Gitchie Manitou State Park, *Thorne 14234* (SMU, UC). Palo Alto Co.: Highland Township, *Hayden 10081* (PH, UC, US). Wayne Co.: Corydon City Reservoir, *van Bruggen 2716* (UC). COLORADO: Baca Co.: 23 mi S of Walsh, *Stephens & Brooks 21788* (DS). Cheyenne Co.: 17 mi N of Kit Carson, *Stephens & Brooks 22662* (DS). Douglas Co.: Wolhurst, *Clokey 3827* (CAN, DS, F, GH, MO, NY, PH, POM, RM, SMU, UC, US, WTU). Elbert Co.: 4 mi SW of Limon, *Ownbey 1301* (COLO, GH, MO, NY, RM, UC). Kiowa Co.: 1 mi E of Eads, *Stephens & Brooks 22703* (DS). Kit Carson Co.: 5 mi E of Flagler, *Stephens & Brooks 22641* (DS). Logan Co.: E of Sterling, *Mathias 333* (MO, POM). Phillips Co.: 5 mi S of Holyoke, *Stephens & Brooks 24072* (DS). Prowers Co.: 20 mi S and 7 W of Holly, *Stephens & Brooks 21931* (DS). Sedgwick Co.: 1 mi S of Julesburg, *Stephens & Brooks 24059* (DS). Yuma Co.: Wray, *Eggleston in 1919* (F, MO, POM). KANSAS: Barber Co.: 3 mi W and 5 mi N of Medicine Lodge, *McGregor 14430* (KANU, SMU, US). Clark Co.: 8 mi S of Sitka, *Rydberg & Imler 766* (KANU, MO, NY). Ellis Co.: 2 mi W of Hays, *Bondy 97* (ARIZ, CAN, F, GH, OKL, OKLA, PH, RM, SMU). Ellsworth Co.: 1 mi N and 1 W of Kanapolis, *Fearing & Latham in 1950* (GH, KANU, TEX, US). Ford Co.: Ca. 5 mi WNW of Dodge City, *Towner 159* (DS). Grant Co.: High upland prairies, *Thompson 1* (CAN, F, NY, UC, US). Harvey Co.: 8.5 mi E of Newton, *Harms 1633* (SMU, UC). Kearney Co.: 5 mi E of Kendall, *Rydberg & Imler 1059* (KANU, NY). Kingman Co.: 3 mi E of Kingman, *Stephens 11127* (OKLA). Meade Co.: 11 mi E of Meade, *Hubert 3593* (KANU, OKLA). Montgomery Co.: 2 mi S of Sycamore, *McGregor 12839* (KANU, NY). Pottawatomie Co.: State Park No. 2, *Marsh 1725* (KANU, SMU, US). Riley Co.: Stony hills, *Norton 168* (GH, MO, NMC, NY, RM, US). 12 mi N of Manhattan, *Raven & Gregory 19483* (DS). Scott Co.: 10.6 mi N of Scott City, *Towner 160* (DS). Smith Co.: 2 mi W of Cedar, *Horr E131* (COLO, F, GH, KANU, LL, OKL, OKLA, RM, SMU, UC, US). Wilson Co.: 3 mi NW of Neodesha, *McGregor 4306* (GH, KANU, US). MISSOURI: Atchison Co.: No locality, *Bush 10321* (GH, PH, POM). Iron Co.: Deo Arc, *Smith 460* (F). OKLAHOMA: Alfalfa Co.: 3 mi N and 7.8 E of Cherokee,

Stratton 6371 (OKL, OKLA). Atoka Co.: No locality, *Hopkins et al. 1132* (OKL, RM, WTU). Blaine Co.: Roman Nose State Park, *Goodman & Waterfall 4189* (OKL, OKLA). 21.5 mi W of Kingfisher, *Towner 153* (DS). Carter Co.: 4 mi N of Springer, *Waterfall 705* (OKL, OKLA, POM). 11.5 mi S of Davis, *Towner 144* (DS). Ca. 7 mi E of Fox, *Towner 143* (DS). Cimarron Co.: 4 mi N of Kenton, *Rogers 5697* (OKL, TEX, US). Comanche Co.: Boggy Hollow Creek, *Eskew 1743* (OKL, OKLA). Dewey Co.: W of Vici, *Goodman 2573* (GH, MO, NY, OKL, POM, RM, WTU). Ellis Co.: Near Shattuck, *Clifton 3155* (GH, NY, OKLA). Greer Co.: 2 mi S of Mangum, *Robbins 3035* (OKL, SMU, UC). 6 mi S of Mangum, *Towner 80* (DS). 2.7 mi S of Mangum, *Towner 83* (DS). Harmon Co.: 13.5 mi W of Mangum, *Waterfall 7766* (OKL, OKLA, TEX). Harper Co.: Near Buffalo, *Stevens 536* (DS, GH, NY, OKL, OKLA, SMU). Kingfisher Co.: 8 mi E of Okeene, *Kelting 250* (KANU, OKL, UC). Lincoln Co.: 6.5 mi S of Perkins, *Towner 148* (DS). 3.2 mi S of Perkins, *Towner 149a* (DS). Logan Co.: 18.8 mi N of Guthrie, *Towner 150* (DS). Major Co.: Togo, *Demaree 12370* (MO, POM). 1.7 mi NE of Orienta, *Raven & Gregory 19471* (DS). Murray Co.: Davis, *Demaree 12508* (GH, MO, NY, OKL, PH). Turner Falls, *Cory 59044* (OKLA, SMU). 6.2 mi E and 2.3 N of Sulfur, *Towner 146* (DS). 8.1 mi S of Davis, *Towner 145* (DS). Oklahoma Co.: 2 mi W of Wood, *Waterfall 2772* (GH, OKL, OKLA). Pontotoc Co.: 1.5 mi NE of Lawrence, *Robbins 2995* (OKL, SMU, UC, WTU). Roger Mills Co.: Ca. 8 mi E of Strong City, *Towner 155* (DS). Tulsa Co.: W of Tulsa, *McKelvey 2508* (GH, POM). Woods Co.: Between Cimarron and Waynoka, *Goodman & Waterfall 4229* (COLO, KANU, OKL, OKLA). TEXAS: Anderson Co.: Palestine, *Palmer 13426* (MO). Andrews Co.: 21–23 mi NE of Andrews, *Correll 32786* (LL). Aransas Co.: 4.6 mi NE of Rockport, *McCart 5566* (TEX). Copano Bay, sandy beach, *Bogusch S-75* (US). 1.3 mi W of Copano Village, near shore of Copano Bay, *Towner 182* (DS). Armstrong Co.: Ca. 10 mi NE of Wayside, *Rowell 5402a* (OKLA). Austin Co.: Colbert's Station, Industry, *Sheldon 3575* (F). Bailey Co.: 5 mi NW of Muleshoe, *Correll 13105, 13106* (LL, SMU). Brazoria Co.: 11.6 mi S of San Luis Pass Bridge on road to Surfside, *Towner 173* (DS). Brazos Co.: College Station, *Parks in 1946, 1947* (RSA, TEX). NW of Bryan, in prairie, *Lundell & Lundell 11304* (POM, SMU). 3.5 mi S of College Station, *McVaugh 6997* (F, LL, SMU). Calhoun Co.: Magnolia Beach, *Tharp in 1930* (TEX). 0.1 mi from shore at Magnolia Beach, *Towner 178* (DS). Cameron Co.: Stover Point, Laguna Atascosa National Wildlife Refuge, *Traverse 1125* (SMU, TEX). Boca Chica, *Lundell & Lundell 8617* (DS, GH, LL, NY, POM, SMU). Brownsville, *Fisher 41188* (ARIZ, NEB). 0.8 mi N of bridge from mainland on Padre I., *Towner 189* (DS). Childress Co.: 10 mi N of Childress, *Correll & Johnston 16876* (LL). Cochran Co.: 14 mi N of Bronco, *Towner 137* (DS). 10.3 mi N of Bronco, *Towner 136* (DS). Collin Co.: Near Plano, *Lundell & Lundell 9313* (DS, GH, LL, POM, SMU). Cooke Co.: 5 mi N of Gainesville, *Gould 6867* (MO, SMU, TEX, UC). Dallam Co.: 1 mi SE of Texline, *York & Rodgers 192* (SMU, TEX, UC). Dallas Co.: Dallas, *Reverchon 3563* (NY). Denton Co.: 5 mi N of Denton, *Cory 57359* (SMU). Eastland Co.: Ranger, *Robinson in 1931* (POM). Erath Co.: Stephenville State Park, *Hoisington in 1946* (TEX). Fannin Co.: Bonham, *Milligan s.n.* (NMC). Galveston Co. (?): Galveston I., *Bechdolt in 1870* (PH). Gray Co.: McLean, *Craig in 1934* (POM). Grayson Co.: Near Gunter, *van Meter 18* (SMU). Hale Co.: 7 mi S of Plainview, *Gould 7156* (SMU). Hall Co.: Memphis, *Thames 7192* (TEX, US). Hardeman Co.: Acme, *Russel 88* (TEX). Hartley Co.: 3 mi SE of Dalhart, *Cory 32667* (POM). Hood Co.: Near Center Mills, *Blackwell 26* (NY, SMU). Hutchinson Co.: Borger, *Hope 4* (LL). Jack Co.: 2.5 mi NE of Jacksboro, *Hennen 421* (SMU). Jackson Co.: 11.2 mi W of Palacios, *Towner 175* (DS). Johnson Co.: S of Rio Vista, *Lewis 4* (SMU). Kleberg Co.: Beach along Laguna Madre, Laureles Division of King Ranch, *Johnston 53224.13* (TEX). Padre I., *Cory 49120* (GH, LL, SMU). Madison Co.: 3 mi N of North Zulch, *Morgan 39* (TEX). Matagorda Co.: 6.5 mi S of Matagorda, *Towner 174* (DS). Montague Co.: 4 mi N of Nocona, *Whitehouse 10070* (SMU). Montgomery Co.: Willis, *Warner s.n.* (MO). Nueces Co.: Corpus Christi, *Drushel 8932* (MO, NY, US). Corpus Christi, *Heller 1517* (PH, US). Parker Co.: Weatherford, *Tracy 7820* (F, GH, MO, NEB, NY, TEX, US). Parmer Co.: 7.8 mi NW of Farwell, *Rowell 10023* (DS, RSA). Refugio Co.: 4.1 mi SE of Austwell, *Towner 181* (DS). Robertson Co.: 3–4 mi S of Hearne, *Reeves 930* (POM). San Patricio Co.: 2 mi S of Ingleside, *Cutler 920* (OKL, WTU). 3.5 mi S of Ingleside, ca. 0.5 mi from Corpus Christi Bay, *Towner 184* (DS). Smith Co.: Troupe, *Reverchon 2744* (MO, US). Tarrant Co.: Sandy soils, *Reverchon 913* (F, GH, KANU, NEB, NY, PH, UC). Van Zandt Co.: 3 mi E of Wills Point, *Shinners 12381* (COLO, SMU). Walker Co.: Vicinity of Huntsville, *Dixon 569* (F, POM, RM, US). Wise Co.: Near Park Springs, *McCart 1633* (SMU, TEX). NEW MEXICO: Chaves Co.: 8.3 mi W of Caprock, *Towner 134* (DS). De Baca Co.: 11 mi S of Ft. Sumner, *Towner 131* (DS). Eddy

Co.: Lakewood, *Wooton in 1909* (NMC, US). Guadalupe Co.: Halfway between Anton Chico and Santa Rosa, *Arsène & Benedict 16681* (POM, US). Lea Co.: Knowles, *Wooton in 1909* (NMC, US). Roosevelt Co.: 5 mi NE of Portales, *Goodman & Hitchcock 1119* (DS, F, GH, MO, NY, PH, POM, RM, UC). 14.0 mi SW of Elida, *Towner 133* (DS). 8.0 mi E of Taiban, *Towner 132* (DS). San Miguel Co.: Between Las Vegas and Romeroville, *Arsène & Benedict 15458* (POM, US). Union Co.: Perico, *Bartlett 227* (NMC). ARIZONA: Graham Co.: Willow Spring, *Palmer 481* (GH, US). Navajo Co.: 4 mi N of Carrizo, *Pulta & Phillips 1008* (ARIZ, UC). 4 mi SW of Show Low, *Lehto 1072* (ARIZ). Forestdale, 66 mi S of Holbrook, *Slough 83* (US).

MEXICO. CHIHUAHUA: 18 mi N of Rubio, District of Cusihuiriac, *Shreve 7960* (POM, US). TAMAULIPAS: Coastal dunes near Río Grande, *Le Sueur 328* (probably of this species, ARIZ, F, TEX).

This species, the earliest described, cultivated, and illustrated (Hooker, 1825) taxon of *Calylophus*, occurs widely over the North American Plains, and is the most familiar member of the genus, although its breeding system has only recently been described (Towner, 1970b). Permanent translocation heterozygosity, half-sterility of pollen and ovules, self-compatibility, and small flowers enhancing self-fertilization are present in *C. serrulatus* as part of the genetic system of complex structural heterozygosity. This type of breeding system is frequent in the Onagraceae, but in *Calylophus* is restricted to this species. Characters associated with this breeding pattern are used as the primary basis for distinguishing *C. serrulatus* from *C. berlandieri*.

Whether factor complexes exist and are maintained in *C. serrulatus* by gametic lethals was not determined. The presence of gametophytic half-sterility makes the involvement of gametic lethals appear likely, but does not exclude mechanisms utilizing megaspore competition and/or zygotic lethals. Although unlikely, the observed levels of pollen and ovule sterility may stem from random chromosome disjunction and the resulting genetic deficiencies and duplications in the gametes. There were no consistent reciprocal differences in pollen fertility, morphology, or chromosomal configurations in hybrids between *C. serrulatus* and *C. berlandieri*, results which would be expected if gametic lethals regulated the transmission of factor complexes. A system utilizing self-sterility alleles combined with egg lethals (see Steiner, 1956, 1957) does not seem to be operating in *C. serrulatus*. All reciprocal crosses between *C. serrulatus* and the self-incompatible species *C. berlandieri* produced only self-compatible hybrids, whereas some self-sterile progeny would be predicted if *C. serrulatus* had retained a functional self-sterility allele.

The flowers of *C. serrulatus* are generally identical to those of *C. berlandieri* except for their smaller size, relatively shorter filaments and style, and the position of the stigma. The placement of the stigma among or near the anthers and early dehiscence of the anthers frequently causes flowers to self-pollinate before anthesis. Undisturbed flowers in the greenhouse showed a high level of autogamous seed set. The similarity of the flowers of the two species extends to morning anthesis times and the ultraviolet-absorbing areas on the petals, stigma, and stamens. Morning anthesis had been known from the first observation of the species by Nuttall (in Hooker, 1825), and was seen and reported again by Stevens (1920), but this was apparently not known to Munz (1965) or Raven (1964). Both mentioned only vespertine anthesis for *Calylophus*. Insects do not

seem to visit *C. serrulatus* frequently. Stevens (1920) observed that bees ignored *C. serrulatus*, although they were active on nearby plants of *Gaura* and *Oenothera*. In my own collecting at 31 colonies of *C. serrulatus*, done at all times of day, no insects were observed visiting flowers. Halictid bees (*Agapostemon*, *Evylaeus*, *Dialictus*) were observed during the morning at one population in Major Co., Oklahoma (P. Raven, personal communication), however.

Meiotic configurations of 34 individuals from 28 populations consisted of a definite or probable ring or chain of 14 chromosomes. Five plants had a ring or chain of 12 chromosomes plus 1 bivalent. Seventeen plants from 5 populations were examined and found to be self-compatible. In *Calylophus* the correlation of self-compatibility and complex structural heterozygosity was found to be nearly perfect. Two exceptions were individuals of *C. berlandieri* having a ring of 12 plus a bivalent at meiotic metaphase I.

With a broad range of phenetic variation which largely overlaps that of *C. berlandieri*, *C. serrulatus* cannot be reliably diagnosed without the use of floral characters or pollen fertility. Parallel geographical variation in vegetative parts is such that near most areas of contact, the two species are quite similar. This implies that *C. serrulatus*, almost certainly a derivative of *C. berlandieri*, is of multiple origins, has experienced secondary local introgression from the parental species or has responded in a similar fashion to natural selection. Much of this vegetative variation in *C. serrulatus* follows a smooth east-west cline, whereas the variation is more discontinuous in *C. berlandieri*. Thus the discontinuities in the parent species are not reflected in the derivative.

Populations formerly assigned to *C. australis*, because they closely resemble adjacent populations of *C. berlandieri*, and by their relative geographical separation from the bulk of *C. serrulatus*, may be an exception to the introgression hypothesis. They could well have been independently derived from *C. berlandieri*. In this paper they are synonymized because no firm knowledge is available on the phylogeny of other populations of *C. serrulatus*. Thus, to preferentially recognize *C. australis*, with scant genetic or morphological support, is to ignore possible polyphyly in the rest of *C. serrulatus*. Instead, *C. serrulatus* is best recognized as a complex assemblage of populations having a common breeding system. These populations encompass a broad morphological diversity, and some of them may have been evolved separately from the bulk of the species.

Variation in *C. serrulatus* involves leaf size and shape, stature, pubescence, and flower size. Flower size is variable throughout the geographical range. Some of the largest-flowered forms occur near large-flowered populations of *C. berlandieri* subsp. *pinifolius* in central Oklahoma. Although the vegetative characters are clinally distributed, most populations occurring west of approximately 98°W longitude are comprised of well-branched, short-leaved, and relatively low-statured plants. East of that line plants are generally less branched, taller and more erect, long leaved, and more densely strigose-canescens.

A few representatives of the eastern form are the following: Davis, Murray Co., Oklahoma, *Demaree 12508* (GH, MO, NY, OKL, PH). Elmore, Farribault Co., Minnesota, *Pammel 596* (GH, MO, RM, US). Near Plano, Collin Co., Texas, *Lundell & Lundell 9313* (DS, GH, LL, POM, SMU). Examples of the western

phenotypes are: 1 mi S of Texline, Dallam Co., Texas, *York & Rogers 192* (SMU, TEX, UC). Wolhurst, Douglas Co., Colorado, *Clokey 3827* (CAN, DS, F, GH, MO, NY, PH, POM, RM, SMU, UC, US, WTU). Moose Jaw, Saskatchewan, *Turner 48* (GH, NY, POM, RSA). Representatives of the coastal Texas populations formerly assigned to *C. australis* include all specimens cited above from Brazos, Austin, Galveston, Brazoria, Matagorda, Jackson, Calhoun, Refugio, Aransas, San Patricio, Nueces, Kleberg and Cameron cos.

Observed instances of direct contact between *C. serrulatus* and *C. berlandieri* were rare. No hybrid zones or populations were identified unequivocally, and the two species were locally allopatric. The only evidence obtained concerning possible mixed populations or direct contact came from the following collections: 3.2 mi S of Perkins, Lincoln Co., Oklahoma, *Towner 149* (DS), one short-styled plant seen in a population of long-styled *C. berlandieri* subsp. *pinifolius*, one of which had a ring of 12 chromosomes and one pair at meiosis. 11.1 mi S of Perryton, Ochiltree Co., Texas, *Towner 158* (DS), chromosome counts of 3 pairs + ring of 4, and possible ring of 12 + 1 pair from the same population, thus perhaps some individuals of *C. serrulatus* in a population of *C. berlandieri* subsp. *berlandieri*. 11.2 mi W of Palacios, Jackson Co., Texas, *Towner 175* (DS), this was a population of *C. serrulatus* which was only 2.2 mi E of a colony of *C. berlandieri* subsp. *berlandieri* (*Towner 176*), the two being identical except for pollen counts and the longer style lengths in the latter population.

Sympatry of *C. serrulatus* with members of sect. *Salpingia* is frequent. In the southern Great Plains, *C. hartwegii* subsp. *fendleri* is often found near or adjacent to populations of this species. Less commonly, *C. hartwegii* subsp. *pubescens* and *C. lavandulifolius* occur with *C. serrulatus* in the same region and at the eastern base of the Rocky Mountains. Lastly, in eastern and southeastern New Mexico, *C. hartwegii* subsp. *filifolius* occasionally comes in contact with *C. serrulatus* on calcareous plains east of the Pecos River. In none of these cases has any evidence of introgression or hybridization been observed.

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